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Amphibia Zambesiaca 3. Rhacophoridae and Hyperoliidae

by

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ABSTRACT

A treatment is given of the taxonomy and distribution of members of the treefrog and reedfrog genera *Chiromantis, Leptopelis, Kassina, Kassinula, Afrixalus* and *Hyperolius* occurring in Botswana, Caprivi, Zambia, Malaŵi, Mozambique and Zimbabwe.

INTRODUCTION

The completion of Parts 1 and 2 of Amphibia Zambesiaca (Poynton & Broadley 1985*a* and 1985*b*) coincided with the final drafting of *Amphibians of the world* (Frost 1985). The nomenclature appearing in Parts 1 and 2 of Amphibia Zambesiaca agrees with the listings in that work, and in the present Part 3 of Amphibia Zambesiaca, entries in *Amphibians of the world* are not included in the tables of synonymy, since this major work is accepted as a standard reference. The nomenclature appearing in this Part again agrees with the listings in *Amphibians of the world*, apart from new names which have appeared in the genera *Leptopelis* and *Afrixalus*. The entries *Afrixalus brachycnemis* and *A. pygmaeus* also differ.

Currently there are extraordinary taxonomic difficulties attached to the study of African treefrogs and reedfrogs, and the present study makes a point of showing areas of unfinished taxonomic business. At the same time, these animals are extraordinarily attractive, interesting and challenging, as evidenced by the very large reference section at the end of this Part, and we hope that the present treatment will prove to be more stimulating than confounding. The keys provided here must be treated with particular caution. Keys are indeed most misleading among the very species where help is most needed, these species being ones where the great range of variation or indefiniteness of features makes simple characterisation artificial. Especially in the genera *Leptopelis, Afrixalus* and *Hyperolius*, the reader can at best be guided to species groups within the respective genera, and for *Hyperolius* a guide to species groups is in fact provided rather than a key. The diagnosis given with each species is intended to be the starting point for identifications.

As stated in the Introduction to Part 1 of this series, this study concentrates on the species level, and is not much concerned with current controversies regarding 'higher' classification. The arrangement of species into genera in this study follows the recent revision of the hyperoliids by Drewes (1984). This does not necessarily imply that a position is taken here regarding Drewes' treatment in all respects. His treatment is at least well reasoned and workable.

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Literature references, locality grid references and acronyms for museum holdings which were given in Parts 1 and 2 of this study are not repeated. We again express our thanks to many colleagues acknowledged in earlier Parts for their ready assistance in this project, and again to Mrs M. E. du Plessis for her painstaking work in preparing the final typescript. Professor D. E. van Dijk and Mr A. J. L. Lambiris critically read the typescript. Discussions with Drs J-L. Perret and R. A. Stevens regarding *Leptopelis*, and with Mr M. Pickersgill regarding *Afrixalus*, are acknowledged. The illustration of the holotype of *Leptopelis parbocagii* sp. n. was prepared by Mr D. M. Dhlamini. The Natal Museum has continued to provide a full range of facilities for the project, and the University of Natal Research Fund has awarded a further publication grant for this Part.

KEY TO THE GENERA OF ZAMBESIACA TREEFROGS

1	Hand with opposable digits	**Chiromantis** (p. 164)
—	All digits set in one plane	2
2	Pupil horizontal to round	**Hyperolius** (p. 193)
—	Pupil vertical	3
3	Vomerine teeth present	4
—	Vomerine teeth absent	5
4	Opening of vent directed ventrally	**Kassina** (p. 178)
—	Opening of vent normally positioned	**Leptopelis** (p. 167)
5	Fingers with webbing	**Afrixalus** (p. 185)
—	Fingers without webbing	**Kassinula** (p. 184)

SYSTEMATIC LIST

Species	*Recorded occurrence*						
	Botswana	*Caprivi*	*Zambia*	*Malaŵi*	*Mozambique*	*Zimbabwe*	*Page*
RHACOPHORIDAE							
Genus *Chiromantis* Peters							
C. xerampelina Peters	●	●	●	●	●	●	165
HYPEROLIIDAE							
Genus *Leptopelis* Günther							
L. flavomaculatus (Günther)	—	—	—	●	●	●	168
L. mossambicus Poynton	—	—	—	●	●	●	169
L. parbocagii sp. n.	—	—	●	●	●	—	171
L. bocagii (Günther)	—	●	●	—	—	●	174
L. sp.	—	—	—	●	—	—	175
L. broadleyi Poynton	—	—	—	●	●	●	176
L. cynnamomeus (Bocage)	—	—	●	—	—	—	177

SYSTEMATIC LIST—*cont.*

Species	*Recorded occurrence*						
HYPEROLIIDAE	*Botswana*	*Caprivi*	*Zambia*	*Malaŵi*	*Mozambique*	*Zimbabwe*	*Page*
Genus *Kassina* Girard							
K. maculata (Duméril)	—	—	—	●	●	●	178
K. kuvangenis (Monard)	—	—	●	—	—	—	179
K. senegalensis (Duméril & Bibron)	●	●	●	●	●	●	180
Genus *Kassinula* Laurent							
K. wittei Laurent	—	—	●	—	—	—	184
Genus *Afrixalus* Laurent							
A. brachycnemis (Boulenger)	—	—	—	●	—	—	187
A. delicatus Pickersgill	—	—	—	—	●	—	188
A. sp.	—	—	●	●	—	—	189
A. crotalus Pickersgill	—	—	—	●	●	●	190
A. aureus Pickersgill	—	—	—	—	●	—	191
A. wittei (Laurent)	—	—	●	—	—	—	191
A. fornasinii (Bianconi)	—	—	—	●	●	●	192
Genus *Hyperolius* Rapp							
H. tuberilinguis Smith	—	—	—	●	●	●	194
H. platyceps major Laurent	—	—	●	—	—	—	195
H. pictus Ahl	—	—	●	●	—	—	195
H. k. kivuensis Ahl	—	—	●	—	—	—	196
H. q. quinquevittatus Bocage	—	—	●	●	—	—	197
H. quinquevittatus mertensi Poynton	—	—	●	●	—	—	198
H. kachalolae Schiøtz	—	—	●	—	—	—	199
H. argus Peters	—	—	—	●	●	●	199
H. puncticulatus (Pfeffer)	—	—	—	●	—	—	201
H. mitchelli Loveridge	—	—	—	●	●	—	203
H. spinigularis Stevens	—	—	—	●	—	—	204
H. pusillus (Cope)	—	—	—	●	●	●	205
H. viridis Schiøtz	—	—	●	—	—	—	206
H. nasutus Günther	●	●	●	●	●	●	206
H. benguellensis (Bocage)	●	—	●	●	—	●	208
H. parkeri Loveridge	—	—	—	—	●	—	211
H. bocagei Steindachner	—	—	●	—	—	—	212
H. marmoratus taeniatus Peters	—	—	—	●	●	●	214
H. marmoratus broadleyi Poynton	—	—	—	—	●	●	216
H. marmoratus marginatus Peters	—	—	●	●	●	●	218
H. marmoratus swynnertoni FitzSimons	—	—	—	—	●	●	219
H. marmoratus rhodesianus Laurent	—	—	—	—	—	●	220
H. marmoratus pyrrhodictyon Laurent	—	—	●	—	—	—	220
H. marmoratus alborufus Laurent	—	—	●	—	—	—	221
H. marmoratus aposematicus Laurent	—	●	●	—	—	●	221
H. marmoratus angolensis Steindachner	●	●	●	—	—	—	222
H. marmoratus argentovittis Ahl	—	—	●	—	—	—	223

SYSTEMATIC LIST—*cont.*

Species	*Recorded occurrence*						
	Botswana	*Caprivi*	*Zambia*	*Malaŵi*	*Mozambique*	*Zimbabwe*	*Page*
HYPEROLIIDAE							
Genus *Hyperolius* Rapp.							
H. marmoratus bitaeniatus Ahl	—	—	●	—	—	—	224
H. marmoratus rhodoscelis (Boulenger)	—	—	●	—	—	—	224
H. marmoratus melanoleucus Laurent	—	—	●	—	—	—	225
H. marmoratus albofasciatus Hoffman	—	—	—	●	●	—	226
H. marmoratus nyassae Ahl	—	—	—	●	—	—	226

Family RHACOPHORIDAE

Pupil horizontal. Vomerine teeth present. Firmisternous pectoral girdle, metasternum a long, bony style. Fingers and toes with intercalary cartilages and discs. Ten genera recognised by Dubois 1981 in Africa, Madagascar and Asia.

The current conception of the family Rhacophoridae originates from Liem's study of the Old World treefrogs (1970), where a diagnosis and definition of the family may be found. There is some recent discussion of the family by Dubois (1981) and Drewes (1984). The family is represented by only one, widespread species in the southern third of Africa, *Chiromantis xerampelina* Peters.

Genus *Chiromantis* Peters

Chiromantis Peters, 1854:626. Type by monotypy: *C. xerampelina* Peters 1854. Liem 1970:91, Dubois 1981:255.

Foam-nest Treefrog. Three species of large-sized, grey to brown coloured treefrogs recognised in Africa. The arrangement of the fingers is distinctive: the outer two are set in a line almost at right angles to the line of the other two, and are separated by a wide space. J. P. Loveridge (1970) showed that 60–80 per cent of the dry weight of urine is composed of uric acid in *C. xerampelina*, and that loss of mass due to desiccation is extremely slow in a drying atmosphere, being similar to that of *Chamaeleo*. As discussed by Coe (1974), the genus shows many adaptations to relatively arid conditions: uricotelism, rectal water resorption and coarse, dry skin. The laying of eggs in foam nests above pools of water need not be seen as an adaptation to aridity: Coe (1974) observes that foam nests have a seeming advantage in conferring a freedom from predation in the early stages of development. Huntly (1985), however, reports egg masses being eaten by Samango monkeys in the Lengwe National Park, Malaŵi. An assessment of the relative amount of predation in water and on land in the egg and early tadpole stages would be a difficult but most interesting study.

Chiromantis xerampelina Peters

Chiromantis xerampelina Peters, 1854:627. Tete and Sena, Mozambique. Syntypes in the Zoologisches Museum, Berlin. Peters 1882:170, Pfeffer 1892:23, Boulenger 1910:529, Hewitt 1911:222, Hewitt & Power 1913: 170, Parker 1930: 899, FitzSimons 1935:392 & 1939: 42, Loveridge 1953*a*:340, Poynton 1964*a*:157 & 1964*b*:214 & 1966:25, Stewart 1967:177, J. P. Loveridge 1970:1, Broadley 1971:119, Coe 1974:26, Stevens 1974:9.

Chiromantis umbelluzianus Ferreira, 1921:205. Umbeluzi Bridge, Maputo district, Mozambique. Type destroyed in the Museu Bocage, Lisbon.

Diagnosis and description. A large treefrog, maximum size up to 90 mm, with opposable digits in the hand (see under discussion of genus). Overall coloration grey to brownish, in strong light becoming almost white. Webbing shows clinal variation: in Malaŵi it tends to join the disc of the outer finger, but to the south and west (ie southern Mozambique, Botswana and Zambia) it normally reaches only as far as the tubercle of the outer finger. Eggs laid in a mass of froth whipped up by the male and female; deposited on virtually any object overhanging water.

Habitat. Common in dry savanna at low altitudes; particularly common in Mopane woodland. During the dry season individuals hibernate in quite exposed places in trees or shrubs, and they are often found in or on buildings, perched on a lamp bracket, picture frame or shelving. Adaptations to arid conditions are discussed under the heading of the genus.

Distribution. Northern Natal, eastern and northern Transvaal across to north-eastern Namibia. Zambia, Zimbabwe, Mozambique, Malaŵi, Tanzania, coastal Kenya.

Localities. BOTSWANA. 65 km NW Francistown (NMZB), Goha Pan (NMZB), Kudumane (TM), Magogaphate Game Camp (NMZB), 25 km NW Martins Drift (TM), Mosu (TM), Nata (NMZB), 16 km S Nata (NMZB), Sikwane (NMZB), 64 km NNW Sikwane (NMZB). CAPRIVI. Katima Mulilo (TM). ZAMBIA. Chakwenga River (NMZB), Chikowa (NMZB), Chilole River (BM), Chipangali (NMZB), Chipata (NMZB), Chiwanda (BM), Chunga (NMZB), Kalichero (NMZB), Kalikali (NMZB), Kalikali/Kongwe (NMZB), Kamilonga Farm (AJL), Kasusu (NMZB), Kapamba River Mouth (BM), Katete/Lupande (NMZB), Kelimba (BM), Livingstone (AMNH, BM, NMZB), Luano Valley (BM), Luembwe/Luangwa (NMZB), Mazabuka Boma (NMZB), Mfuwe (NMZB), Mkanda (NMZB), Monze (NMZL), Moshi Camp (NMZB), Mufue (NMZB), Mulanga (NMZB), Mwanachanda (BM), Nchelenge (BM), Ngoma (NMZB), Nsefu Game Camp (NMZB), Sayiri Court (NMZB), Sitwe (NMZB). MALAŴI. Kamazu Academy (BM), Lake Kazuni (BM), Lake Pamalombe (BM), Mangochi (BM), Misuku Hills East (NMZB), Nyungwe (NMZB), Salima (NMB). Blantyre; Chitala; Chowe; Limbe; Mtimbuka; Thyolo; Zomba (Loveridge 1953*a*). Rumpi (Stewart 1967). MOZAMBIQUE. Alves de Lima (NMZB), Amamba (NMZB), Amatongas (NMZB), Charre (BM), Chibabava (NMZB), Chitiaca (NMZB), Dondo (NMZB), 7 km S Estatuane (NMZB), Guija (TM), Guro (NMZB), Ichope (NMZB), Jofane (NMZB), Jorge (NMZB), 25 km N Lower Revue Bridge (NMZB), Mabote (TM), 30 km SE Machailla (TM), Magasso (NMZB), Magude (TM), Mananga (DM), Massangena (NMZB), Mitucué Mountain (NMZB), 15 km S Muanza (NMZB), Muda/Lamego (NMZB), 20 km SW Mungari (NMZB), 10 km SSE Ressano Garcia (NMZB), Ribaue Mountain (NMZB), Sena (ZMB), Sofala

Bay (BM), Tete (NMZB, ZMB), 72 km ENE Tete (NMZB), 97 km N Tete (BM), Umbeluzi River (TM), Vila Fontes (Zanue River) (NMZB), 15 km SE Vila Franca do Save (NMZB), Xiluvo (NMZB). Quelimane (Pfeffer 1892). ZIMBABWE. Antelope (NM), Bangala Dam (NMZB), Bindura (NMZB), Birchenough Bridge (TM), Buffalo Range (NMZB), Bulawayo (Hillside) (NMZB), 19 km S Bulawayo (NMZB), 16 km SSW Chakari (AJL), Charara Confluence, Kariba (NMZB), Chete Gorge (NMZB), Chibuwe (NMZB), Chinhoyi (NMZB), Chipinda Pools (NMZB), Chiredzi (NMZB), Chirivira Falls (NMZB), Cyrene (NMZB), Fatima (NMZB), Fishan (NMZB), Fothergill Island, L. Kariba (AJL), Gandavaroyi Falls (NMZB), Gem Farm (AJL), Guluene South, Gonarezhou (NMZB), Gwanda (NMZB), Inyati C.L. (NMZB), Inyazura (NMZB), Jalopi River, Hwange (NMZB), Kandahar Fishing Camp (NMZB), Kanyemba (NMZB), Kariba (NMZB), 20 km NNE Kariba, Zambezi River (AJL), 24 km W Kariba Dam (NMZB), KweKwe (NMZB), Lukosi (NMZB), Lundi River Bridge (NM), Mabalauta Field Station (NMZB), Machiniwa Pan (NMZB), Mahenya (NMZB), Main Camp, Hwange G.R. (NMZB), Majinji Pan (NMZB), Makuti (NMZB), Malugwe Pan (NMZB), Mana Pools (NMZB), Mangune Pan (NMZB), Marhumbini (NMZB), Masvingo (NM, NMZB), Matusadona N.P. (Nyameni River) (NMZB), Mhangura (NMZB), Mpakati (NMZB), Mutare (AM), Mutoko (AM, NM), 8 km W & 51 km NE Mutoko (NMZB), Mwenezi (NMZB), Ngamo Pans (NMZB), Ngezi C.L. (NMZB), Nottingham Ranch (NMZB), Ntabambomvu (NMZB), Nyala Pan (NMZB), 6 km W Nyampanda (NMZB), Nyamuweni Pan (NMZB), Nyanyadzi (NMZB), Ranelia Farm (NMZB), Razi Dam (NMZB), Ruware (NMZB), Sabi/Lundi Confluence (NMZB), 5 km W Sanyati River Mouth, L. Kariba (AJL), Sazale Pan (NMZB), Sengwa Estuary (NMZB), Sengwa River (NMZB), Sengwa Sound, Kariba (NMZB), Sentinel Ranch (NMZB), Shashi Irrigation Scheme (NMZB), Sinamatela (NMZB), Umgusa River Bridge (NMZB), Wanganella Farm (AJL), Westwood Vlei (NMZB), Zambezi River (Hwange Pump Station) (TM).

Family HYPEROLIIDAE

Pupil vertical (at least in the primitive state: Drewes 1984) to horizontal. Vomerine teeth present (at least in the primitive state: Liem 1970) to absent. Firmisternous pectoral girdle, metasternum a thin cartilaginous plate. Fingers and toes with intercalary cartilages and discs. Fourteen genera recognised by Drewes (1984) in Africa and associated islands.

Discussion of the family may be found in Liem (1970), Dubois (1981) and Drewes (1984). Following Drewes, five genera are recognised in the Zambesiaca area. The family is particularly notorious for the taxonomic problems it presents at the species level. The largest genus, *Hyperolius*, has caused many expressions of dismay in the past, but the situation within this genus now appears to be reasonably satisfactory, at least in comparison with difficulties still existing in other genera, especially *Leptopelis* and *Afrixalus*. The present lack of material and of critical field data inhibits taxonomic assessment, and particularly in the case of *Leptopelis* and *Afrixalus*, it appears that external features alone do not provide adequate data for a workable taxonomy.

Genus *Leptopelis* Günther

Leptopelis Günther, 1858:89. Type by monotypy: *Hyla aubryi* Duméril. Liem 1970:103, Dubois 1981:260, Drewes 1984:56.

Medium to large treefrogs, with tendencies within the genus to become fossorial: *L. bocagii* at the extreme is essentially a ground frog. Pupil vertical. Vomerine teeth present. Omosternum entire to notched posteriorly. Digital discs well developed to absent. Fingers webbed to not webbed; toes webbed, although in some species only very weakly so. Overall coloration in juveniles green (turning bluish in alcohol), becoming brown with a darker n-shaped patch on the back in most species.

No vocal sac or gular gland in males.

The least-derived hyperoliid genus according to Drewes (1984), primarily forest dwelling and arboreal, but with a savanna-living trend shown in several species. Occurring in most of Africa south of the Sahara, excluding nearly all of Namibia, Botswana, the Transvaal and areas to the south. Eggs large and yolky; oviposition at ground level near (but not in) water in the few species studied, with tadpoles making their own way to water, apparently guided by topographic and humidity gradients (Oldham 1977).

Schiøtz (1975) believed his treatment of *Leptopelis* to be 'grossly inadequate', and the systematics of the genus is still inadequate. Differential characters in the genus are exceptionally difficult to discern, and field studies especially in Malaŵi, Zambia and Angola will have to be well advanced before the present situation can show much improvement. The length of the inner metatarsal tubercle in relation to the inner toe, or to some other measure, has commonly been used as a differential character, but it appears to be subject to positive allometry: it tends to become relatively larger the larger the specimen. Consequently the length of this tubercle can be compared only among specimens of about the same size. Even so, the range of variation shown by this character is considerable. Allometry, as Parker (1936) and Laurent (1973) have noted, is detectable in several other characters.

The presence or absence of pectoral glands in males is used in this study as a 'character' in the diagnoses of species. As Schmidt & Inger (1959) have shown, this is a seasonal feature, and its absence in a specimen need not necessarily mean that the specimen cannot be referred to any species diagnosed as having pectoral glands. The 'character' should therefore be used with circumspection.

Key to the Zambesiaca species of *Leptopelis*

Caution! Comments about keys in the Introduction should be noted.

1 Broad web between outer fingers reaching proximal tubercle of outer finger **flavomaculatus** (p. 168)
— No or virtually no webbing between fingers 2
2 Width of disc of fourth toe greater than width of toe's distal subarticular tubercle 3
— Width of disc not greater than width of subarticular tubercle 5
3 Length of metatarsal tubercle > 80 % length of inner toe (distribution centred on the Mozambique Plain) 4

— Length of metatarsal tubercle ≮ 80 % length of inner toe (distributed in western Zambia and Angola) .... **cynnamomeus** (p. 177)

4 Horizontal diameter of tympanum > half diameter of eye .... **mossambicus** (p. 169)

— Horizontal diameter of tympanum < half diameter of eye . **broadleyi** (p. 176)

5 No dorsal pattern in adult.......................... **Leptopelis** sp. (p. 175)

— Dark n- or m-shaped pattern on back 6

6 Interorbital distance/distance from nostril to tympanum not more than 36 % **bocagii** (p. 174)

— Ratio 36 % or more .... **parbocagii** (p. 171)

Leptopelis flavomaculatus (Günther)

Hyperolius flavomaculatus Günther, 1864*a*:310. Rovuma Bay. Tanzania. Holotype in the British Museum (N.H.) London.

Hylambates johnstoni Boulenger, 1897:803. Kondowe to Karonga, Malaŵi (restricted by Loveridge 1953*a*). Syntypes in the British Museum (N.H.) London.

Leptopelis johnstoni; FitzSimons 1939:43.

Leptopelis flavomaculatus; Loveridge 1953*a*:343, Poynton 1964*a*:168 & 1964*b*:214 & 1966:25 & 1985*b*:466, Stewart 1967:119, Stevens 1974:9, Schiøtz 1975:37.

Diagnosis. Length of third finger 70–85 % distance from nostril to tympanum, width of disc of fourth toe more than 120–170 % width of distal subarticular tubercle, length of metatarsal tubercle more or less equal to length of inner toe, tubercle moderately flanged. Broad web between third and fourth toes reaching to usually passing distal subarticular tubercle of toe 3; between fourth and fifth toes reaching to usually passing distal tubercle of toe 5. Broad web between outer fingers reaching more than midway along proximal tubercle of outer finger, usually passing it. Males with pectoral glands.

Description. A large treefrog (body length of females up to 70 mm, males up to 50 mm), with a relatively large tympanum (horizontal diameter more than half diameter of eye, larger in females than in males), and with well-developed digital discs. Fairly extensive webbing between toes, a small amount of webbing between the outer fingers. Juveniles a uniform green dorsally with a scattering of yellow spots. Adults tend to lose the body spots at a size of about 45 mm, and are either a uniform green or, more usually, overall brown with a darker n-shaped patch and an interocular bar. Retention of the green coloration appears to occur only in males (Schiøtz 1975).

Habitat. Characteristic of evergreen forest from sea-level up to 1 600 m. Males often call from leaves or branches three or four metres from the ground, but on Vumba Mountain calling has been heard apparently from below ground. At the Rusitu Lagoon, large numbers of males were calling from low branches and shrubs only one or two metres above a shallow boulder-strewn side channel. *L. broadleyi* was also abundant in this area. At high altitudes (Stapleford and Vumba Mountain) this species occurs at low densities, probably due to the shortage of suitable breeding sites within montane forest.

Females are rarely collected. One was found on the ground in Dondo Forest.

Remarks. Laurent (1973) treated *L. lebeaui* Witte as a subspecies of *flavomacula-*

tus, although no explicit reasons for doing so were given. Examination of the *lebeaui* holotype (RGMC 5146) shows the webbing to be less extensive than is usual in *flavomaculatus*, although it does fall within the quite considerable range of variation. The length of the inner metatarsal tubercle falls within the range of variation of *flavomaculatus* specimens of the same size, but it is not flanged as sharply as in *flavomaculatus*. In disc size, the *lebeaui* holotype falls outside the range of variation of *flavomaculatus*: disc/toe width ratio varies from 125 % to 155 % in *flavomaculatus*, but it is only 100 % in the *lebeaui* holotype. It appears that the finger- and toe tips of the *lebeaui* holotype are slightly desiccated, but even taking this into account, the difference in disc size seems substantial. Nothing useful is gained by treating this poorly known taxon as a subspecies of *flavomaculatus* (Laurent does not in fact list *lebeaui* separately in his 1973 revision of *Leptopelis* in Zaïre), and, in a genus where only very slight morphological differences are of taxonomic significance, the differences in metatarsal shape and disc size argue against Laurent's procedure. We provisionally regard *lebeaui* as a separate species, badly in need of more study.

Distribution. Mozambique north of the Save River, the eastern Zimbabwean escarpment, Malaŵi, eastern Tanzania, coastal Kenya.

Localities. MALAŴI. Kondowe/Karonga (BM), Nkhata Bay (NMZB), Ruo Gorge (NMZB). Forestry Houses, Katendeza, Kawiya and Lake Dambo in the Chintheche area (de Fonesca & Jocque 1979); Mulanje dist., (Stevens 1974). MOZAMBIQUE. Amatongas (NM, NMZB), Chiniziua dist. (NMZB), Dombe Forest (NMZB), Dondo (NMZB), 15 km NNW Dondo (NMZB), Garuso (NMZB), Gorongoza Mountain (NMZB), Makurupini River (NMZB), Nicuadala (NMZB). ZIMBABWE. Chirinda Forest (BM, NM, NMZB, TM), Haroni Forest (NMZB), Haroni River (NMZB), Haroni/Rusitu confluence (Rusitu Lagoon) (NMZB), Ngorima Reserve (East) (NMZB), Pungwe Bridge (NMZB), Stapleford (NMZB), Vumba Mountain (NMZB).

Leptopelis mossambicus Poynton

Leptopelis johnstoni (not Boulenger 1897); Parker 1930:900, Cott 1932:479.
Leptopelis concolor (not Ahl 1929); Poynton 1964:169 (part: all except some specimens from Xiluvo & 8 km NE Dondo).
Leptopelis viridis cinnamomeus (not Bocage 1893); Poynton 1966:27 (part: Vila Bocage).
Leptopelis lebeaui (not Witte 1933); Stevens 1974:9.
Leptopelis ? cinnamomeus (not Bocage 1893); Schiøtz 1975:24 (part: Mozambique & Zimbabwe).
Leptopelis ? lebeaui (not Witte 1933); Schiøtz 1975:26 (Stevens' 1974 material).
Leptopelis mossambicus Poynton, 1985*b*:467. Maputo, Mozambique. Holotype in the Natal Museum, Pietermaritzburg.

Diagnosis. Length of third finger 65–88 % distance from nostril to tympanum, width of disc of fourth toe 104–140 % width of distal subarticular tubercle, length of metatarsal tubercle 90–130 % length of inner toe (positive allometry is marked), strongly flanged. Broad web between third and fourth toes reaching midway to the distal subarticular tubercle of toe 3 to falling well short of it; between fourth and fifth toe reaching level of distal tubercle of toe 5, rarely just falling short. Males with pectoral glands.

Description. A medium- to large-sized treefrog (body length of females up to 63 mm, males up to 52 mm), with a relatively large tympanum (horizontal diameter more than half diameter of eye), and with moderately developed digital discs. Limited webbing between toes, virtually none between fingers. Dorsal ground colour a light brown, with a usually very conspicuous n-shaped dark brown band from near occiput to urostyle (see Remarks). The area contained within this band may be almost completely darkened, but usually there is a large central area about the same shade as the rest of the ground colour. Dark ocular patches are occasionally present, rarely joined to form an interocular bar. Juvenile a uniform green dorsally.

Habitat. Savanna to open reedbeds, in the vicinity of rivers or swamps. Males call usually from thin branches or reeds, a variable height above ground.

Remarks. As with other *Leptopelis* species, the markings in *mossambicus* are variable and show clinal tendencies. The dorsal patch is most clearly defined in southern (i e South African) specimens. Material collected from the area of Beira and the Zambezi-Shire basin shows variation from a clear dorsal patch to a faint outline, or a mere scattering of freckles, or no clear dorsal markings at all. The three adult types from Maputo include quite a wide part of the range of variation: in NM 3681 the patch is clearly defined and most of the central area between occiput and sacrum is darkened; in NM 3682 (holotype) the outer border of the patch is clearly defined but most of the central area is not darkened; in NM 3680 the marking shown on the holotype is somewhat disrupted, tending towards the freckled condition of more northern material. Material from south-eastern Zimbabwe shows similar variation to Beira material, the dorsal patch being barely discernible in a few specimens. Small dark ocular patches, rarely joined by an interocular bar, occur in some specimens from the more central part of the range.

On the tibiae, clearly defined dark patches are usually (but not invariably) present in South African material, but such markings are absent (or at least extremely faint) in northern material. They are very faintly shown on the holotype. The dark dorsolateral band diminishes in length from south to north, but much variation can be shown in a single series, as in the type series: in the holotype the band is continuous from the canthal region to the sacral area of the dorsal patch on one side, while in NM 3681 it does not even extend as far as the position of the elbow when folded on one side.

In northern material, individuals occur with a relatively greater disc diameter than is found in southern material. The distal subarticular tubercle of the fourth toe varies from being a single to a paired structure in South African material, while in northernmost material it is a single structure, at most only slightly bifurcated. The relative width of this tubercle is unaffected by the variation, however, and consequently the use of the standard disc/tubercle ratio seems valid in this species. In the Maputo type series the tubercle is entire to bifurcate.

Distribution. Lowlands of northern Natal, Swaziland, Transvaal, Mozambique, Zimbabwe and southern Malaŵi.

Localities. MALAŴI. Chikwawa (RS). MOZAMBIQUE. Beira (BM, NM, NMZB), Charre (BM), Chimonzo (TM), Chiniziua District (NMZB), Dondo (NMZB), Fambani River (BM), Inchope (NM, NMZB), Inhamitanga (NMZB), Lower Revue Bridge (NMZB), Manga (NMZB), Maputo (NM), Muda/Lamego

(NMZB), Ponte do Pungwe (NMZB), Pungwe Bridge (NM), 25 km SE Ressano Garcia (NMZB), Vila Bocage (NMZB), Vila Fontes (NMZB), Xiluvo (NMZB, TM), Zavora (NMZB, TM). ZIMBABWE. Chiredzi (NMZB), Jersey Estate (NMZB), Machaniwa Pans (NMZB), Mahenya (NMZB), Malugwe Pan, Gonarezhou (NMZB), Ngorima Reserve (East) (NMZB), Rupembi Swamp (NMZB).

Leptopelis parbocagii sp. n. Fig. 1

? *Leptopelis bocagei* (not Günther 1864); Parker 1936:97 (part).
Hylambates bocagii (not Günther 1864); Hoffman 1942:180.
Leptopelis bocagii (not Günther 1864); Loveridge 1953*b*:342, Poynton 1964*b*:214, Stewart 1967:122.
Leptopelis bocagei lebeaui (not Witte 1933); Schmidt & Inger 1959:176 (part: not material from Kabwe and Nsombo in Zambia).
? *Leptopelis angolensis* (not Bocage 1893); Poynton 1964*b*:214, Stewart 1967:121.
Leptopelis viridis cinnamomeus (not Bocage 1893); Poynton 1966: (part: specimens from Chapala, 8 km NE Nicuadala, Ribaue Mountain, Chilongulelo, Mpulungu, Mulosa, Zomba), Linden 1971:237, Stevens 1974:9.
Leptopelis lebeaui (not Witte 1933); Broadley 1971:120.
? *Leptopelis bocagei* (not Günther 1864); Stevens 1974:9.
Leptopelis ? *cinnamomeus* (not Bocage 1893); Schiøtz 1975:24 (part: Mozambique uplands, Malaŵi, Zambia).

Types. Holotype: a gravid female in the collection of the Musée Royale de l'Afrique Centrale, Tervuren, R. G. Mus. Congo 101088, collected at Mabwe, eastern shore of Lake Upemba, Zaïre (alt. 585 m) on 26 November 1948 by the Mission G. F. de Witte. Identified as *Leptopelis bocagei lebeaui* (Witte) by R. F. Inger. Paratypes: four females in the collection of the Musée Royale de l'Afrique Centrale, R. G. Mus. Congo 101005–7 and 101082, collected from the same

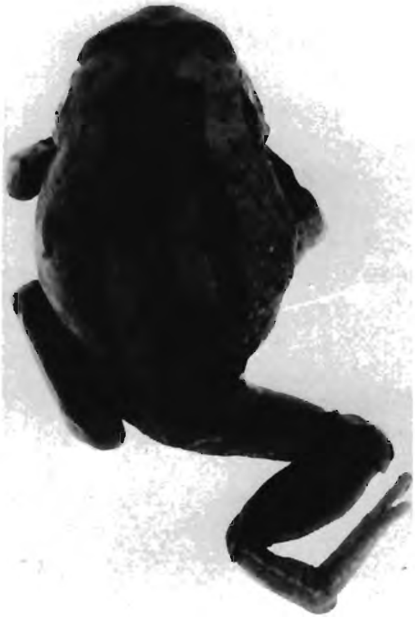

Fig. 1. *Leptopelis parbocagii* sp. n. holotype (RGMC 101088), Mabwe, east of Lake Upemba, Zaïre. Natural size.

locality between 28 July 1947 and 18 December 1948. Also identified by Inger as *Leptopelis bocagei lebeaui.*

Dimensions of holotype in mm: snout to urostyle tip 59,2; width of head 26,2; snout tip to angle of jaw 19,8; nostril to tympanum 14,1; horizontal diameter of eye (eye retracted) 6,7; width of eyelid 5,8; interorbital distance 6,7; length of third finger 9,1; width of disc of third finger 1,9; width of distal subarticular tubercle of third finger 1,7; length of tibia 24,8; length of metatarsal tubercle 5,1; length of first toe 4,7; width of disc of fourth toe 2,0; width of distal subarticular tubercle of fourth toe 1,9.

Markings of holotype (Fig. 1): a dark, broad interocular bar forms the base of an inverted triangle whose apex joins a dark n-shaped patch from occipital region to beyond sacrum, also an irregular vertebral band, resulting in an m-shaped dorsal marking. A dark dorsolateral band extends from tympanum to level of folded elbow, and continues as a series of dark spots. No discernible markings on thigh, but a light horizontal line extends above vent. Tibiae with irregular dark patches.

Paratypes agree with holotype, although markings are not so well developed: interorbital bar not connected to dorsal patch, which tends towards fragmentation of m-shaped marking. Smallest specimen, with a snout–urostyle length of 43,9 mm, retains a light longitudinal line on lateral surface of arm and foot, the latter being continuous with supra-anal light band when legs are folded. Allometric relationships, noted in the discussion of the genus, are evident in this series: in the smallest specimen the length of the metatarsal tubercle is only 103 % the length of the inner toe (adults show a value of 106 % or more), and the width of the disc of the fourth toe is 121 % the width of the distal subarticular tubercle (< 111 % in adults).

Diagnosis. Length of third finger 55–75 % distance from nostril to tympanum, width of disc of fourth toe 80–108 % (rarely over 100 %) width of distal subarticular tubercle, length of metatarsal tubercle 106–134 % length of inner toe, strongly flanged. Interorbital distance greater than in *bocagii*: interorbital distance/distance from nostril to tympanum 36 % or more (see Remarks). Broad web between third and fourth toes just reaching distal subarticular tubercle of toe 3 to (more usually) falling well short of it; between fourth and fifth toes just reaching to falling short of distal tubercle of toe 5. Males with pectoral glands.

Description. A medium- to large-sized 'treefrog' with ground-living tendency (see discussion in Linden 1971). Body length of females up to 64 mm but usually not reaching 60 mm, males up to 54 mm, with a relatively large tympanum (horizontal diameter more than half diameter of eye), and with discs barely developed to absent. Very limited webbing between toes, none between fingers. Dorsal ground colour a light brown, with a conspicuous n-shaped dark brown band from near occiput to urostyle. The area contained within the band varies from having dark, mainly longitudinally arranged marbling (typically including a vertebral band, often resulting in an overall m-shaped dorsal marking) to virtually complete darkening. Dark interocular bar usually present, but tending to be reduced to separated ocular patches in the southern part of the range. Juveniles a uniform green dorsally.

Habitat. A savanna species, showing 'progressive adaptation to the fossorial habit'

(Linden 1971:240). Males call from reeds or bushes, or from ground level (see Remarks).

Remarks. The literature subsequent to Schmidt and Inger's important study of the Upemba Park amphibians (1959) has not accepted these authors' assignation of the present species either to *bocagii* or to *lebeaui* (eg Laurent 1973, Poynton 1985*b*). Following Laurent (1957), the name *viridis cinnamomeus* (or *cynnamomeus*) became adopted, but Perret (1976) stated that this usage was not consistent with what he observed in the now destroyed type of *cynnamomeus* Bocage, not does it appear to be consistent with what is known of the distribution of the species concerned (Poynton 1985*b*). Bocage's *cynnamomeus* is evidently restricted to an area from southern Angola to Lake Mweru (see under *L. cynnamomeus*), an area that appears to lie outside the range of the species which Laurent took a lead in calling *cynnamomeus*. Material evidently referable to this latter species has been recorded by Laurent (1964) from northern Angola, and material which cannot be separated by known characters from the Upemba series has been collected from northern Zambia, Malaŵi and upland areas of northern Mozambique (Poynton 1985*b*). As the Upemba collection has been treated as the main reference material for this particular species, it seems logical, in the absence of any available name, to designate one of the series from this collection as types of this species, named *parbocagii* because of its similarities with *bocagii* Günther.

Differences between this species (under the name of *viridis cynnamomeus*) and *bocagii* have been discussed by Laurent (1973) in Zaïre material. Laurent found differential characters in the width of the digital discs, the length of the third finger and the upper eyelid: interorbital space ratio. He noted, however, that these characters are influenced by allometry, and in practice it cannot be expected that any specimen coming to hand can necessarily be assigned with confidence to one or other species using the current diagnostic characters. Indeed, some of the specimens in the Zambesiaca area which we have assigned to one or other species may prove to be wrongly identified should more effective differential characters be discovered.

It is also distinctly possible that in Malaŵi, at least, the material which we have assigned to *parbocagii* includes another as yet undescribed species. Stevens (1974) listed his Malaŵian material under two different species, '*viridis cinnamomeus*' and '*bocagei*', although he noted that the material possibly represents 'ecological demes of the same taxon'. His *cinnamomeus* males were found calling from vegetation, while his *bocagei* males were found calling from ground level. Stevens (1974) assigned material from the Palombe–Tuchila Plain to *bocagii*, but an examination of Plains material in the Natural History Museum, Bulawayo, agrees with *parbocagii* rather than *bocagii* at least in respect of eyelid and interorbital measurements employed by Laurent (1973), and so for the moment the material is included in *parbocagii*. The width of the eyelid and of the interorbital space is not possible to measure with great precision owing to uncertain demarcation between the two, and the eyelid: interorbital relationship used by Laurent (1973) is itself not particularly effective as a differential character: a wide overlap is indeed shown in Laurent's fig. 4. The interorbital distance divided by the distance from nostril to tympanum appears to provide better separation, *bocagii* giving a value of not more than 36 %, while *parbocagii* gives a value of 36 % or more, at least in the material so far examined. The Plains material in the Natural History Museum gives a value of 37 % or more, apart from one specimen from Lifupa, which gives a value of 35 %. Stevens (in litt.) has himself come to the view that true *bocagii* does not occur in southern Malaŵi. Loveridge (1953*a*) reported *bocagii* in this area; the two specimens in his collection (MCZ 27201 & 27202) have been examined and are here assigned to *parbocagii*.

Distribution. Uplands of northern Mozambique and Malaŵi, northern Zambia, northern Angola, Zaïre; northern part of range uncertain owing to taxonomic confusion.

Localities. ZAMBIA. Chilongowelo (BM, NMZB), Mbala (IRSN), Mporokoso (IRSN, PEM), Mpulungu (BM), Mweru Wantipa (IRSN). MALAŴI. Chisambo (NMZB), Chitala (NMB), Lifupa (NMZB), Lilongwe (NMZB), Limbe (Hynde Dam) (NMZB), Nchisi Mountain (MCZ), Thyolo Mountain (MCZ), Zomba (BM, NMZB). Blantyre (Linden 1971). MOZAMBIQUE. Chapala (NMZB), Nicuadala (NMZB), Ribaue Mountain (NMZB).

Leptopelis bocagii (Günther)

Cystignathus bocagii Günther, 1864:481. Duque de Bragança, Angola. Syntypes (Perret 1976) destroyed in the Museu Bocage, Lisbon.

Leptopelis bocagei haasi Mertens, 1937:21. Nsombo, Zambia. Holotype in the Senckenberg Museum, Frankfurt.

Leptopelis bocagei lebeaui (not Witte 1933); Schmidt & Inger 1959:176 (part: material from Kabwe and Nsombo).

Leptopelis bocagei; Poynton 1964*a*:172 & 1964*b*:215, Schiøtz 1974:14.

Leptopelis bocagii; Broadley 1971:120.

Diagnosis. Length of third finger 54–70 % distance from nostril to tympanum, width of disc of fourth toe 80–100 % width of distal subarticular tubercle (rarely 100 %), length of metatarsal tubercle 105–140 % length of inner toe, strongly flanged. Interorbital distance less than in *parbocagii*: interorbital distance/distance from nostril to tympanum not more than 36 % (see Remarks under *L. parbocagii*). Broad web between third and fourth toes just reaching to (more usually) falling short of distal subarticular tubercle of toe 3; between fourth and fifth toes reaching to (more usually) falling short of distal tubercle of toe 5. Males with pectoral glands.

Description. A moderately sized 'treefrog' (body length of females up to 58 mm in the Zambesiaca area, males up to 50 mm) with pronounced ground-living tendency, with a relatively large tympanum (horizontal diameter half or more than half diameter of eye), and with weakly developed discs (width not exceeding width of digits) or (more usually) with tips of fingers and especially toes tending to taper. Webbing between toes rudimentary, absent between fingers. Dorsal markings varying from a dark n-shaped band with some additional banding mid-dorsally (often forming an overall m-shaped dorsal pattern), to a uniformly darkened dorsal patch, which may be so extensive as to cover the whole head. Where this extreme is not shown, a dark interocular bar is usually present, but it may be reduced to two separate supra-orbital patches. Juveniles with a uniform green to brown-green dorsum.

Schmidt & Inger (1959) note an absence of the common *Leptopelis* feature of a supra-anal light line in *bocagii*. While this is the usual condition in *bocagii*, weak development of the line in occasional specimens from various parts of the Zambesiaca area precludes it being used as a diagnostic character. Its occurrence in *parbocagii* and *mossambicus* is also not invariable.

Habitat. A savanna species, with strong fossorial tendencies. Abundant in areas of occurrence, but emerging and calling only in wet weather. Typically calling at ground level, but one of us (J. C. P.) collected a specimen (NM 3685), seemingly referable to *bocagii* on morphological grounds, calling on a dead bush two metres from the ground at the Lundi River Bridge (Rhino Hotel), Zimbabwe, during very wet weather.

Distribution. According to current taxonomic understanding (which may be faulty in that more than one natural species is included), distributed mainly on higher ground from Ethiopia to northern Namibia and Zimbabwe (and the northern Transvaal, judging from a specimen in the Transvaal Museum, TM 31142, from Letsitele).

Localities. CAPRIVI. Western Caprivi (NMZB). ZAMBIA. Chipata (NMZB), Chunga (NMZB), Isombo Stream (NMZB), Kabwe (BM), Kafue N.P. (NMZB), Kalabo (AMNH, CNHM), Kalomo (BM), Kamilonga Farm (AJL), Kasusu (NMZB), Lusaka (NMZL), Mkanda (NMZB), Monza (NMZL), Mporokoso (PEM), Mwekera (NMZB), Nsombo (SMF), Salujinga (AMNH), Sayiri (NMZB), Siantamba (NMZB). ZIMBABWE. Atlantica R.S. (AJL), Audley End Farm (AJL), Banti Forest Reserve (NMZB), Beverley Hills (AJL), Braeside (NMZB), Bulawayo (Hillside) (NMZB), Chisawasha (AM, SAM), Christon Bank (NMZB), Elim Mission (NMZB), Ellesmere Farm (AJL), Gokwe (NMZB), Harare (AJL, AM, NMZB), 15 km W Harare (NMZB), Kadoma (AJL), Karoi (NMZB), Kutama (AJL), KweKwe (NMZB), Lundi River Bridge (NM), Mabelreign (NMZB), Malemi Dam (NMZB), Mangula (NMZB), Marlborough (NMZB), Matopos (NMZB), Meyrick Park (NMZB), Miller's Creek, Lake McIlwaine (NMZB), Mount Hampden (NMZB), Mutare (NMZB), Mutoko (NM), 52 km NE Mutoko (NMZB), Mvurwi (NMZB), Ranelia (NMZB), Saffron Walden (NMZB), Selborne (NMZB), Selukwe (NMZB), Udu Dam (NMZB), Westwood Vlei (NMZB), Zimbabwe Ruins (NMZB).

Leptopelis sp.

Leptopelis sp. Stevens 1974:9. Chiradzulu district, Malaŵi.
Leptopelis sp. 1 Schiøtz 1975:26.

A uniform green or uniform brown *Leptopelis* was discovered by Stevens (1974) among reeds in the Chiradzulu district. The material bears closest resemblance to *L. parbocagii*, and a report is being prepared by Stevens. The material also recalls the uniformly coloured *L. parvus* Schmidt & Inger (1959) from the Upemba Park, but *parvus* has more extensive webbing, reaching the subarticular tubercles of the third and fifth toes (falling well short of these tubercles in the Chiradzulu material).

Localities. MALAŴI. Chiradzulu district (RS), ?Makoka A.R.S. (BM).

Leptopelis broadleyi Poynton

Leptopelis concolor (not Ahl); Poynton 1964:169 (part: some specimens from Xiluvo & 8 km NE Dondo) & 1966:25, Stevens 1974:9.

Leptopelis argenteus meridionalis Schiøtz, 1975:22. 8 km NE Dondo, Mozambique. Holotype in the Natural History Museum, Bulawayo.

Leptopelis broadleyi Poynton, 1985*b*:468 (new name: *meridionalis* preoccupied by *L. calcaratus meridionalis* Laurent 1973).

Diagnosis. Length of third finger 70–80 % distance from nostril to tympanum, width of disc of fourth toe 133–162 % width of distal subarticular tubercle, length of metatarsal tubercle 84–98 % length of inner toe, strongly flanged. Broad web between third and fourth toes level with distal subarticular tubercle of toe 3; between fourth and fifth toes level with distal tubercle of toe 5, sometimes only just reaching these tubercles. No webbing between fingers. Males lacking pectoral glands.

Description. A relatively small treefrog (body length of females up to 52 mm, males up to 45 mm) with a small tympanum (horizontal diameter less than half diameter of eye), and with well-developed discs. Limited webbing between toes, none between fingers. Discs with conspicuously darker coloration on upper surface. Dorsal ground colour a light brown, with a darker pattern of an interorbital triangle, the apex pointing backwards and tending to continue as a pair of bands diverging over the scapular region. The central area of the back contained within these bands has scattered dark patches. The interorbital triangle and diverging scapular bands may be traced only as discontinuous patches. A very discontinuous dark line commencing at tip of snout, following canthus rostralis and continuing behind eye. Juveniles show light speckling, which is retained up to a body length of 20 mm or more.

Habitat. Common in areas of forest–savanna mosaic and along forested streams flowing through savanna, frequently sympatric with *L. flavomaculatus*. Stevens (1974) describes the species as 'arboreal', collected in 'lightly-wooded dambos in Mulanje district'. Males usually call from small trees or bushes at a height of between one and two metres.

Remarks. As discussed by Poynton (1985*b*), this form had to be renamed on account of the name *meridionalis* becoming preoccupied just prior to the publication of Schiøtz's description. Specific status seems preferable on account of this form differing in morphology from *L. concolor* Ahl, noted by Poynton (1966) and Schiøtz (1975), and differing in markings from *L. argenteus* (Pfeffer), noted by Schiøtz (1975) (Poynton 1985*b*).

Distribution. Extreme eastern Zimbabwean lowland, Mozambique north of the Save, southern Malaŵi.

Localities. MALAŴI. Chisambo (NMZB), Mulosa (Malosa) (JV, RS). MOZAMBIQUE. Chapala (NMZB), Chiniziua dist. (NMZB), Dondo, 8 & 16 km NE Dondo (NMZB), Inhamitanga (NMZB), 8 km NE Nicuadala (NMZB), Xiluvo (NMZB). ZIMBABWE, Ngorima Reserve (East) (NMZB).

Leptopelis cynnamomeus (Bocage)

Hylambates cynnamomeus Bocage, 1893:120. Quilenges, Angola. Holotype (Perret 1976) destroyed in the Museu Bocage, Lisbon.
Leptopelis moeroensis Laurent, 1973:29. Pweto, Lake Mweru, Zaïre. Holotype in the Musée Royal de l'Afrique, Tervuren.
Leptopelis sp. Schiøtz 1975:51.
Leptopelis cynnamomeus; Perret 1976:22, Poynton 1985*b*:467.

Diagnosis (based on only nine specimens). Length of third finger 74–82 % distance from nostril to tympanum, width of disc of fourth toe 125–164 % width of distal subarticular tubercle, length of metatarsal tubercle 59–80 % length of inner toe, rounded to weakly flanged. Broad web between third and fourth toes level with the distal subarticular tubercle of toe 3; between fourth and fifth toes level with, to just passing, distal tubercle of toe 5. Virtually no webbing between fingers. Males with weakly developed pectoral glands.

Description. A relatively small treefrog (body length of males up to 38 mm) with a moderately large tympanum (horizontal diameter slightly less to slightly more than half diameter of eye), and with well-developed discs. Fairly limited webbing between toes, but toes have a fringe of webbing; virtually no webbing between fingers. Dorsal ground colour brown, with a (sometimes indistinct) darker pattern of an interorbital bar and a pair of bands diverging posteriorly over the scapular region. The central area of the back contained within these bands has scattered dark markings. The interorbital bar may form the base of an inverted pyramid, the apex of which joins the diverging scapular bands. A well-marked dark line commences at the tip of the snout, follows the canthus rostralis and continues behind the eye to about the scapular region; accentuated by a light line lying dorsal to it. Two juveniles still with tails show the dark interorbital bar and the light dorsolateral lines.

Habitat. No data available.

Remarks. As discussed by Perret (1976), Poynton (1985*b*) and under *L. parbocagii* (p. 173), the name *cynnamomeus* has evidently been incorrectly applied to material which includes the species *parbocagii* and *mossambicus*. Comparison of a paratype of *L. moeroensis* (RGMAC 112694) with the available Zambian material reveals no features that allow separation. *L. moeroensis* was described before Perret (1976) published his findings on the type material of *cynnamomeus*. Schiøtz (1975) noted that the call of this species is very similar to the call of members of the *argenteus* group, and in markings, disc development and webbing also, there are strong similarities between *broadleyi* and *cynnamomeus*. The presence of pectoral glands in *cynnamomeus* does, however, separate this species from the *argenteus* group.

Distribution. As discussed by Poynton (1985*b*), the species has been known from southern Angola and the north-western corner of Zambia. The inclusion of *moeroensis* in the synonymy extends this range to Lake Mweru. As Laurent (1973) noted, it is not known to occur elsewhere in Zaïre.

Localities. ZAMBIA. Ikelenge (NMZB), Isombu (NMZB), Salujinga (AMNH).

Genus *Kassina* Girard

Kassina Girard, 1853:421. Type by monotypy: *Cystignathus senegalensis* Duméril & Bibron. Priority over *Hylambates* granted by Opinion 849, *Bull. zool. Nomencl.* **25**:20, 1968. Liem 1970:104, Dubois 1981:216, Dubois, Morère, Stimson & Clarke 1983:114, Drewes 1984:53, Opinion 1364, *Bull. zool. Nomencl.* **42**:355, 1985.

Hylambates Duméril, 1853:162. Type by monotypy: *H. maculatus* Duméril. Liem 1970:106.

Cassina Cope, 1864:182.

Cassiniopsis Monard, 1937:41. Type by monotypy: *Cassiniopsis kuvangensis* Monard.

Large (not exceeding 70 mm) to moderately large ground frogs. Pupil vertical. Vomerine teeth present. Omosternum forked posteriorly. Inner metatarsal tubercle usually poorly developed, not strongly flanged. Digital discs well developed to absent. Fingers without webbing, toes almost half-webbed to poorly webbed. Tendency for basal phalanx of fifth toe to become bound to fourth.

Male with a single vocal pouch, with prominent gular gland either free or attached posteriorly (so dividing the vocal pouch externally). Opening of vent in both sexes, but particularly in female, tending to be ventrally directed. The functional significance of this requires investigation.

Occurring practically throughout Africa south of the Sahara, but poorly represented in true forest. Although no southern African species can be called a treefrog, a strong tendency to climb is shown, and *K. maculata* normally hibernates in wild or domestic banana axils. Eggs are laid in water in the species that have been studied. Drewes (1984) recognised eleven species of *Kassina*, three of which occur in the Zambesiaca area.

Key to the Zambesiaca species of *Kassina*

Caution! Comments about keys in the Introduction should be noted.

1 Tips of fingers and toes expanded into flattened discs, broader than the width of the subarticular tubercles .... **maculata** (p. 178)
— Expanded discs not present 2
2 Width of inner metatarsal tubercle markedly greater than width of subarticular tubercle of first toe, no distinct outer metatarsal tubercle **kuvangensis** (p. 179)
— Width of inner metatarsal tubercle not exceeding width of subarticular tubercle of first toe, outer metatarsal tubercle evident... **senegalensis** (p. 180)

Kassina maculata (Duméril)

Hylambates maculatus Duméril, 1853:165. Zanzibar. Type in the Muséum National d'Histoire Naturelle, Paris. Loveridge 1953*a*:343, Poynton 1964*a*:173 & 1964*b*:215 & 1966:29, Stewart 1967:123.

Kassina maculata; Stevens 1974:9, Schiøtz 1975:58.

Diagnosis. Size large (not usually exceeding 65 mm, metamorphosing usually above snout–vent length of 35 mm). Tips of fingers and toes expanded into flattened discs, broader than width of subarticular tubercles. Length of inner metatarsal tubercle less than internarial distance, width not greater than width of subarticular tubercle of first toe. No outer metatarsal tubercle. Basal phalanx of fifth toe usually possessing proximal tubercle, separated from fourth toe along whole length by web. Web just reaching to just passing distal tubercle of third toe. Gular gland in males circular, with a free posterior flap.

Description. Large and treefrog-like in appearance, apart from relatively short hind limbs. Inner metatarsal tubercle weakly developed. Back with large, asymmetrically placed blotches, legs and arms with red ground colour in both sexes when breeding. Underside of legs heavily marbled apart from ventral reticulation on thighs.

Gular skin in breeding males very deeply folded into a single gular pouch, partly covered by a more or less circular gland with a free posterior edge. In non-breeding condition the skin is not folded or formed into a gland except for very slight creases on either side of the gland area. Vent of female directed moderately downwards and opening posterio-ventrally; surrounded by fairly inconspicuous, simple lobes covered by asperities when in breeding condition. Vent of males situated normally, almost directly below urostyle tip.

Habitat. During the dry season, adults and juveniles are commonly found in banana axils. Breeding takes place in pans and dams, the males calling while floating in water, but apart from arboreal tendencies during hibernation, the species is essentially ground-living. It is very common on the eastern lowland plains, but it occurs at the Leopard Rock dams on Vumba Mountain at 1 400 m. The lowland *argyreivittis* form of *K. senegalensis* (p. 181) also occurs at this locality.

Distribution. Eastern lowlands from Kenya to near Durban, South Africa.

Localities. MALAŴI. Chikwawa; Shiré Valley (Loveridge 1953*a*), Nsanje (Stewart 1967), Shiré Valley; Mulanje dist. (Stevens 1974). MOZAMBIQUE. Amatongas (BM), Beira (NM), Boane (TM), Boroma (NMZB), Caia (BM), Chimonzi (TM), Dondo (NMZB), Estatuane (NMZB), Garuso (NMZB), Ibo (BM), Inhamitanga (NMZB), 8 km E of Jangamo (TM), Macia (SAM), Macuti (NMZB), Maputo (NM), Ponte do Calichane (NM). ZIMBABWE. Leopard Rock (NMZB), Marhumbini (NMZB), Majinji Pan (NMZB), Nyamakari (NMZB).

Kassina kuvangensis (Monard)

Cassiniopsis kuvangensis Monard, 1937:41. Kuvangu, Angola. Holotype in the Muséum d'Histoire Naturelle, Geneva.

Kassina ingeri Laurent, 1963:137. Kalabo, Zambia. Holotype in the Field Museum of Natural History, Chicago. Broadley 1971:120. Stjernstedt 1973:196.

Kassina kuvangensis; Schiøtz 1975:61.

Diagnosis. Relatively large (maximum male 51 mm, maximum female 49 mm). Tips of fingers and toes not expanded laterally, even tapering slightly. Length of inner metatarsal tubercle equal to slightly less than internarial distance, width markedly greater than width of subarticular tubercle of first toe. No distinct outer metatarsal tubercle. Basal phalanx of fifth toe usually without a proximal tubercle, bound for at least half its length to fourth toe. Main part of webbing almost reaching distal tubercle of third toe to falling less than half-way between tubercles. Gular gland in males circular to slightly oval (but width not less than 80 % length), without a free posterior flap, but usually clearly demarcated posteriorly by a crease.

Description. Distinctively *Kassina*-like in appearance, but relatively large and with a relatively massive inner metatarsal tubercle. No outer tubercle, back virtually uniform dark or with asymmetrically placed dark blotches, though tending to be arranged in longitudinal series. Underside of entire leg heavily marbled.

Breeding males with a more or less circular gular gland (Schiøtz 1975, fig. 60), demarcated anteriorly and posteriorly by only a crease, with the result that the remaining gular skin is formed externally into paired gular pouches. Vent of female directed strongly downwards, opening right on the ventral surface, and surrounded by very expanded, frilled lobes without asperities. Vent in male also directed ventrally, with a posterio-ventral opening.

Habitat. Common within their range, calling in flat open grasslands covered with a few centimetres of water (Stjernstedt 1973 and in Schiøtz 1975). Taken in the undergrowth of dense miombo woodland at Ikelenge (C. A. Green, field notes).

Remarks. Schiøtz (1975) referred *ingeri* to the synonymy of *kuvangensis*, having examined Monard's type, but mentioned the possibility of its being a synonym of *senegalensis* on account of the spotted back of the *ingeri* types and uniform back of the *kuvangensis* type. But as he noted, the distinctness of dorsal markings in *Kassina* is variable, and Keith's sample of seven specimens (AMNH) certainly confirms this variability. The almost rounded gular gland, and ventral marbling to the legs, shown in the figure of *ingeri*, are alone sufficient to exclude it from *senegalensis* (see also Drewes 1984:41). The matter is discussed further under *senegalensis*.

Distribution. Northern and western Zambia, and at least southern Angola.

Localities. ZAMBIA. Ikelenge (NMZB), Kalabo (AMNH, FMNH, NMZB), Kalenga (NMZB), Mayau River (AMNH), Mukonge (NMZB, NMZL). Lubushi (Schiøtz 1975).

Kassina senegalensis (Duméril & Bibron)

Cystignathus senegalensis Duméril & Bibron, 1841:418. Galam Lakes, Senegal. Syntypes in the Muséum National d'Histoire Naturelle, Paris.

Cassina argyreivittis Peters, 1854:626. Cabaceira and Boror, Mozambique. Syntypes in the Zoologisches Museum, Berlin. Peters 1882:157.

Kassina senegalensis; Parker 1930:900, FitzSimons 1935:392, Loveridge 1953*a*:344, Poynton 1964*a*:175 & 1964*b*:215 & 1966:30, Stewart 1967:125, Broadley 1971:120, Stevens 1974:10, Schiøtz 1975:53, Drewes 1984:55.

Diagnosis. Medium-sized (not normally exceeding 45 mm). Tips of fingers and toes swollen or only slightly expanded laterally. Length of inner metatarsal tubercle less than internarial distance, width not exceeding to slightly exceeding width of subarticular tubercle of first toe. Outer metatarsal tubercle evident. Basal phalanx of fifth toe with proximal tubercle, bound usually more than half its length to fourth toe. Webbing reaching ⅔ way between tubercles of third toe to (rarely) virtually absent, tending to be fleshy. Gular gland in males oval (width *c.* 60 % length) or strap-like, without a free posterior flap and usually not clearly demarcated posteriorly.

Description. Distinctively *Kassina*-like in appearance. Back with a vertebral and a pair of paravertebral dark bands, unbroken or broken into a series of bands or spots. Undersurface of legs immaculate (mainly in western material) to marbled apart from the immaculate ventral thigh area.

Breeding males with an oval or strap-like gular gland, not clearly demarcated anteriorly or (usually) posteriorly by a crease, resulting in externally separated pair of vocal pouches (Drewes 1984, figs 13 & 16B). Vent of female directed strongly downwards, opening on or almost on the ventral surface, and surrounded by papillate lobes, without asperities. Vent in male also directed ventrally, with a posterio-ventral opening.

Habitat. The species hibernates under logs and rocks, and within termitaria. It breeds in shallow temporary pools and pans. The males usually call from under the shelter of grass tufts.

Remarks. Drewes (1984) recently observed that the elucidation of the *K. senegalensis* complex is 'the most perplexing problem' in the genus. The present treatment does not claim to go very far towards elucidation, since more data than those contained in the standard character sets of colour pattern and body shape are needed. Critical field data are especially needed.

Variation in eastern African material has been discussed by Schiøtz (1975). While not proposing the establishment of subspecies, he recognised four different 'forms', of which three occur in south-east Africa. 'Form 1' *(senegalensis)* extends from west Africa through Uganda and western Tanzania to Zambia. It has a normally unbroken dorsal stripe and dorsolateral stripes broken into oblong spots. 'Form 3' *(argyreivittis)*, distributed in the coastal lowlands of southern Kenya and Tanzania, also Mozambique and South Africa, has the dorsal and dorsolateral stripes usually unbroken. He notes (p. 56) that: 'The difference between these southern specimens and those termed form 1 from eg southern Tanzania and Zambia is not great and the two forms may merge into each other in Mozambique–Rhodesia–Malaŵi.'

Examination of south-east African material shows a cline in markings from east to west, best shown if some large series are considered. It is convenient for this purpose to split Schiøtz's Form 3 into *argyreivittis* proper, with unbroken stripes (as illustrated by Peters 1882, pl. 22, fig. 2), and the Form 3 illustrated in Schiøtz's fig. 52, in which there is a symmetrical occipital break in the dorsolateral stripes, leaving a patch above each eye. The term 'Form 3' will be used in this restricted sense.

The proportions of each of the different 'forms' in the largest series available from localities along the Beira–Harare road are shown in the following table:

Locality	No. of specimens	% *arg.*	% *arg.*/F3	% F3	% F3/F1	% F1
Xiluvo	23	84	8	8	0	0
Amatongas	15	46	27	20	7	0
Mutare area	13	15	15	23	39	8
Harare area	14	0	0	14	43	43

Material from Zambia, Botswana, Namibia, the Transvaal and Natal shows the same characteristics as the Harare material. One F3 specimen from Harare shows an expansion of the dorsal band between the eyes, to the extent that it fuses with the patch above the right eye. This interorbital expansion and possible fusion with an eye patch (if present) is taken by Laurent (eg 1976*a*) to be characteristic of *angeli*. Specimens with this feature have been collected in Zimbabwe at Avondale Farm (Masvingo), 18 km south of Bulawayo, and Lupane; and in Zambia at Mayau River and on the Nyambeja and Sandaula Plains. Apart from the single Bulawayo specimen, the others have been collected together with specimens not showing this feature. These markings are also present in ten of the 59 clearly marked near-topotypes (Durban, S. Africa) of *modesta* Ahl, considered a synonym of *senegalensis* (Poynton 1964*a*). Schiøtz's view that such markings have no taxonomic value thus seems confirmed.

It is clear from the above table that Schiøtz was correct in suspecting that his F1 and F3 merged with each other. This merging over eastern Zimbabwe and Mozambique makes it impossible to recognise *argyreivittis* as a subspecies on the basis of markings, and no morphological characters have been detected that provide, in fairly large series, grounds for effectively separating Mozambique from Zambian material. In fact we find no grounds for separating any other forms in southern Africa.

Mertens (1971) proposed reviving *deserticola* for Namibian material, and more recently, Laurent (1976*a*) discussed reviving *modesta* (from Mariannhill, near Durban) and/or *deserticola*. Mertens noted the 'helleren Gesamtfärbung von *deserticola*' (which is not confirmed in topotypic material we have examined), and also 'der plumperen Körperform' of *deserticola*. Laurent noted that in Natal and Transvaal material, 'la tête semble plus large'. The following table gives head width/body length ratios of male topotypic or near-topotypic material of *deserticola*, *modesta* and *argyreivittis*:

	Locality	Number (males)	Pattern	Body length (mm)	Head width/ body length
deserticola	Windhoek	8	F3	37–45	0,32–0,36
modesta	Mariannhill	2	F1	35–36	0,32–0,33
	Durban	9	F1–F3	31–34	0,32–0,34
argyreivittis	Xiluvo	10	*arg.*	32–36	0,32–0,37
	Chapala	3	*arg.*	38–43	0,34–0,36

Such data hardly give grounds for recognising subspecies, and there appear to be no other features that provide surer grounds for separation, even when material from opposite sides of the continent are compared. Thus comparison of three near-topotypic *argyreivittis* from Chapala with eight *deserticola* topotypes reveals no clear morphological differences except for two on the feet. In the Chapala specimens, the first phalanx of the fifth toe is bound along its whole length to the fourth toe, so that its large subarticular tubercle is held firmly against the fourth toe. Furthermore, this tubercle is slightly nearer the large second tubercle of the fourth toe than the small tubercle at its base. In the Windhoek material, the first phalanx of the outer toe is not completely bound to the fourth toe, so its tubercle is separated by fleshy webbing from the fourth toe, and this tubercle is slightly nearer the basal tubercle of the fourth toe. The condition in the Chapala specimens is, however, not a feature of southern Mozambique or Malaŵi material, even of those specimens showing the *argyreivittis* pattern. Specimens with this pattern show variation from the Chapala condition of a fully bound fifth basal phalanx to a loosely bound condition, and a positioning of the larger tubercle from being nearer the second tubercle of the fourth toe to being nearer the basal tubercle. This full range of variation is shown in the Xiluvo series.

The other noticeable difference between Chapala and Windhoek material concerns the inner metatarsal tubercle, which is slightly larger in the Windhoek specimens. Variation from one condition to the other occurs in southern Mozambique series, however, indicating that taxonomic use cannot be made of size difference in this tubercle within the species.

All in all, the available material appears to provide no clear grounds for the separation of taxa within the *senegalensis* complex on the basis of morphology or colour pattern, and we therefore follow Schiøtz in referring all southern material to *senegalensis*.

Note should be taken, however, of a spotted 'Form 4' which Schiøtz describes as occurring in north-eastern Zambia. Western Zambian material shows a range of variation which also includes spotted rather than striped specimens. In two AMNH specimens from the Mayau River, the pattern is an interrupted F1 in the one specimen, and more spotted, approaching F4, in the other. A single FMNH specimen from Kalabo shows an interrupted dorsal stripe. In three NMZB males from the Sandaula Plain, the pattern is an irregular F3 in one, more broken and asymmetrical in another, and in the third composed of completely asymmetrical spots which is a F4 patterning that strongly recalls the *kuvangensis* patterning. Although the inner metatarsal tubercles are relatively large, approaching *kuvangensis*, the gular discs are the elongated *senegalensis* type, there is no sign of *kuvangensis* ventral marbling. Also, outer metatarsal tubercles are present, and no other *kuvangensis* features present themselves. The F4 pattern therefore does not necessarily indicate *kuvangensis* introgression, but the possibility still deserves investigation in areas where the two species are sympatric.

Distribution. Virtually all savanna areas south of the Sahara.

Localities. BOTSWANA. Francistown (TM), 65 km NW Francistown (NMZB), 50 km W Kanye (NMZB), Khwai River (NMZB), Kwikampa (NMZB), Lethlekane (NMZB), Magogophate Game Camp (NMZB), 25 km NW Martins Drift (TM), Masarwanye (NMZB), Maun (NMZB), Okavango Delta (TM), Tselenyane (NMZB), Xaxaba (NMZB). CAPRIVI. Katima Mulilo (TM). ZAMBIA. Bwana Mukubwa (NMZB), Chipangali (NMZB), Chilonoma (BM), Dumdumwenzi (NMZB), Kafue National Park (NMZB), Kalabo (FMNH), Kalenga (NMZB), Karubwe (TM), Kasusu (NMZB), Livingstone (NMZL), Luangwe Valley (NMZB), Mayau River (AMNH), Mbala (BM, TM), Mfuwe (NMZB), Monze (NMZL), Mporokoso (PEM), Nyambela Plain (NMZB), Sandaula Plain (NMZB). 17 km N Kafue River Bridge; nr Kasama; Mazabuka (Schiøtz 1975). MALAŴI. Chikwawa (TM), Lifupa (NMZB), Limphasa Dambo (NMZB), Mangochi (NMZB), Zomba (BM), Zomba Mountain (BM). Blantyre; Dedza; Manchewe Falls (Stewart 1967). MOZAMBIQUE. Amatongas (NMZB), Boror (ZMB), Cabaceira (ZMB), Chapala (NMZB), Chigubo (TM), 10 km NE Dondo (NMZB), 5 km S Estatuane (NMZB), Estatuane (NMZB), Fambani River (BM), Machipanda (NM), Magasso (NMZB), Massangena (TM), Metuchira (NMZB), Muda/Lemego (NMZB), Pico Meponduine (NMZB), Tete (NM), 15 km SE Vila Franco do Save (NMZB), Xiluvo (NMZB). ZIMBABWE. nr Antelope Mine (NM), Avonmore Farm (NMZB), Baddeley (NMZB), Beatrice (NMZB), Bembesi (NMZB), 34 km W Birchenough Bridge (NMZB), Bulawayo (NMZB), 20 km S Bulawayo (NMZB), Bundi Valley (NMZB), Charara Confluence (NMZB), Chivakwe River Bridge (NMZB), Chimwara Ranch (NMZB), Chiredzi (NMZB), Chirivira Falls (NMZB), Chizarira Range (NMZB), Cyrene Mission (NMZB), Dhlodhlo Ruins (NMZB), Dunblane (NMZB), Empress Mine (NMZB), Foliot Farm (NMZB), 50 km NW Gokwe (TM), Gonda's (BM), Gubalala Pan (NMZB), Harare (NMZB), Hwange National Park (NMZB), Insiza T.T.L. (NMZB), Inyanga N.P. (NMZB), Inyati C.L. (NMZB), Kadoma (NMZB), KweKwe (NMZB), Leopard Rock (NMZB), Linkwasha Pan (NMZB), London Farm (NMZB), Longueville Ranch (NMZB), Lough Lyn (NMZB), Lukosi (NMZB), Lundi River Bridge (NM), Lupane (NMZB), Mabalauta F.S. (NMZB), Mabelreign (NMZB), Machinawa Pans (NMZB), Majinji Pan (NMZB), Malapati Drift (NMZB), Maleme Dam (NMZB), Malugwe Pan (NMZB), Mana Pools (NMZB), Mangula (NMZB), Marhumbini (NMZB), Mare Dam (NMZB), Masvingo (NMZB), Matopos N.P. (NMZB), Mhangura (NMZB), Mount Hampden (NMZB), Murewa (NMZB), Musami (AM), Msoro (NMZB), Mutare (NM, NMZB), Mutoko (NM), 60 km NE Mutoko (NMZB), Musirizwi River (NMZB), Ngezi Dam (NMZB), Ngorima Reserve (NMZB), Nyala Pan (NMZB), Nyamugwe Pan (NMZB), Old Umtali (NMZB), Ranelia (NMZB), Rhodes Estate Office (NMZB), Rukomeshe R.S. (NMZB), Rukute Farm (NMZB), Sabi/Lundi Confluence (NMZB), Sable Park (NMZB), Saffron Walden (NMZB), Sanyatwe (NMZB), Selborne (NMZB), Sengwa Gorge (NMZB), Shashi Irrigation scheme (NMZB), Silalabuhwa (NMZB), Silverstreams (NMZB), Teaklands (NMZB), Toronto (NMZB), Udu Dam (NMZB), Umzilizwe River (NMZB), Vumba Mountain (NMZB), Warren Hills (NMZB), Watsomba (NMZB), Westwood Vlei (NMZB), World's View (S), Zimbabwe (NMZB).

Genus *Kassinula* Laurent

Kassinula Laurent, 1940:313. Type by original designation: *K. wittei* Laurent 1940. Drewes 1984:55 & 1985:186, Tandy & Drewes 1985:191.

Minute ground frogs (not exceeding 22 mm, usually less). Pupil vertical. Vomerine teeth absent. Omosternum forked posteriorly. Inner metatarsal tubercle short (less than internarial distance), but fairly wide (wider than width of subarticular tubercle of first toe). Tips of fingers and toes expanded slightly into small discs. Fingers without webbing, webbing reaching less than half-way between tubercles of third toe. Basal phalanx of fifth toe bound for its whole length to fourth toe.

Male with a circular gular gland, with a free posterior flap. A monotypic genus, known from Shaba Province (Zaïre) and adjacent Zambia. Drewes (1984) removed *Kassinula* from the synonymy of *Kassina*, where it has been placed by Laurent & Combaz (1950).

Kassinula wittei Laurent

Kassinula wittei Laurent 1940:314. Kansenia, Kanzenze & Kando, Shaba Province, Zaïre. Holotype in the Musée Royal de l'Afrique Centrale, Tervuren. Drewes 1984:55 & 1985:186, Tandy & Drewes 1985:191.

Kassina wittei; Broadley 1971:120, Schiøtz 1975,64.

Diagnosis and description. See under diagnosis of genus. *Afrixalus*-like in appearance. Digital discs present, but in even slightly desiccated specimens not evident; in well-preserved material made conspicuous by being unpigmented. Subarticular tubercles well developed and an outer metatarsal tubercle usually discernible; basal phalanx of fifth toe with a proximal tubercle. Back with a dark vertebral band, attenuated or interrupted in the middle, and dark paravertebral bands extending from scapular region to base of legs, broadening where middle band narrows. Resulting light bands with a fine dark line running along the middle. Underside immaculate.

Males with a single, large folded gular pouch, partly covered by a circular gland that has a free posterior edge.

Habitat. Occurring in grassy bogs on a granite outcrop near the Zambezi Rapids, Mwinilunga District (C. A. Green, field notes).

Distribution. Uplands of western and northern Zambia and southern Zaïre.

Localities. ZAMBIA. Ikelenge (NMZB), Chitanta Plain, 29 m N Mwinilunga (AMNH), Mungwi, Kasama (BM).

Genus *Afrixalus* Laurent

Afrixalus Laurent, 1944:111. Type by original designation: *Megalixalus fornasinii* (Bianconi). Liem 1970:108, Dubois 1981:261, Drewes 1984:46.

Small- to medium-sized reed- or sedge frogs. Pupil vertical. Vomerine teeth absent. Omosternum forked posteriorly. Fingers and toes webbed and with discs. Marked tendency for development of asperities or spinules in skin of body and limbs of at least males.

Gular gland in males forming a conspicuous disc; no nuptial pad.

Members of this genus are common in open, reeded or grassy swamps and pools. Eggs are usually deposited in jelly within a folded leaf, either above or below water, depending on the species. Some 27 species are scattered over most of subsaharan Africa, but in only the more eastern areas of southern Africa.

Pickersgill (1984) has made a study of features which may be used to distinguish taxa among the southern small-sized forms of this genus. While he found clear ecological and behavioral differences, external features of diagnostic value were found to occur mostly in males in breeding condition, which leaves the identification of much of the available preserved material in a less than satisfactory state. We have largely adopted Pickersgill's taxonomic separation of the available material in the belief that this separation is at least adequate in providing 'species-hypotheses', discussed in the Introduction to Part 1 of this series (Poynton & Broadley 1985*a*). Such hypotheses will hopefully stimulate and facilitate more intensive investigation.

Essentially, the dwarf *Afrixalus* of the Zambesiaca area appear to include two superspecies or complexes. The one has a general covering of skin asperities, and a dorsal pattern composed of a patch in the inter-ocular-occipital area (sometimes including an interocular bar), from which diverge two paravertebral stripes that tend to broaden posteriorly and join a dorsolateral band on each side. This marking is continued on the tibia of the folded leg as an oblique band or patch. We believe these features to be indicated in the *brachycnemis* syntypes, as discussed under that species. Schiøtz (1974 & 1975), however, assigned this form to *pygmaeus*. Pickersgill (1984) described similar southern material as *A. delicatus*.

In the other superspecies or complex, the skin asperities are restricted in area, and there is a lack of a broad interocular-occipital patch. The paravertebral pair of stripes are parallel for the most part, although they tend to converge at one or other end, and they do not usually join the dorsolateral bands at the sides. Tibial markings are absent or longitudinally arranged, or, if oblique, then weakly developed. These features were taken by Schiøtz to be those of *brachycnemis* Boulenger, but in our opinion the syntypes give no positive support for this assignation, as discussed below. Pickersgill described similar southern material as *A. crotalus*. The third species of dwarf *Afrixalus* described by Pickersgill, *aureus*, appears, as discussed below, to show most similarity with *knysnae* to the south.

We do not find these two complexes to be wholly separable: even among Pickersgill's numerous paratypes, we believe that several specimens are dubiously assignable. Yet this indefiniteness appears to reflect a natural state of affairs, recalling the situation described in this study between *Hyperolius nasutus* and *H. benguellensis* (p. 209), as well as other cases discussed by Poynton (1982). Such cases suggest complex and incomplete vicariation events associated with Quaternary disturbances. Standard taxonomic procedures need not be expected to be wholly applicable in such cases, and differences of opinion and uncertainty regarding identification of specimens will be frequent. The museum curator, faced with the alternatives of leaving much of his material unidentified or lumping it all under *'brachycnemis'*, may well, for the present, be inclined to opt for the latter alternative.

Key to the Zambesiaca species of *Afrixalus*

Caution! Comments about keys in the Introduction should be noted, also comments in the above discussion of the genus.

1 Adult body size > 28 mm .... **fornasinii** (p. 192)
— Adult body size < 28 mm 2

2 Dorsal pattern a well-marked pair of dark paravertebral bands meeting over the head, tapering to a sharp point anterior to the eyes; no distinct dorsal markings on the tibia (occurring in western and northern Zambia) ..... **wittei** (p. 191)
— Markings not as above (distributed in eastern and more southern regions) 3

3 Dorsal pattern includes a pair of diverging paravertebral stripes, broadening posteriorly and continued on tibiae of folded legs as oblique band or patch spanning full width of limb .... **brachycnmeis** (p. 187), **delicatus** (p. 188)
— Pattern not as above 4

4 Dark patch present in the interorbital-occipital area, lumber region of each side, and tibiae .... **aureus** (p. 191)
— Markings (if present) in form of elongated stripes or bands .... **Afrixalus** sp. (p. 189), **crotalus** (p. 190)

Afrixalus brachycnemis (Boulenger)

Megalixalus brachycnemis Boulenger, 1896:403. Chiradzulu, Malaŵi. Syntypes in the British Museum (N.H.), London.
Afrixalus brachycnemis brachycnemis; Loveridge 1953*a*:346 (part) & 1953*b*:145, Poynton 1964*b*:216 (part), Stewart 1967:128.
Afrixalus pygmaeus pygmaeus; Schiøtz (? not Ahl) 1974:14 & 1975:87 (part), Stevens 1971:10.

Diagnosis and description (see remarks under genus). Body length not exceeding 25 mm. Minute asperities over dorsal and ventral surface in males, in females confined to head or absent. A dark canthal and dorsolateral band (usually with light speckling) present, including a posterior portion of the upper eyelid. Dorsal pattern, when most complete, comprises a dark elongate patch commencing anteriorly between the eyes (sometimes including an interocular line) and continuing to the occipital area, from where originates a pair of paravertebral bands which diverge somewhat as far as the sacral region and then broaden, joining the dorsolateral bands if they extend that far posteriorly. The occipital patch may show degrees of fragmentation, commencing with a lightening of the central area, and the paravertebral bands also show degrees of fragmentation, to the extent that there are virtually no dark dorsal markings. An oblique band on the tibia continues the paravertebral band when the leg is folded. This band also shows degrees of fragmentation. Schiøtz's figure of '*A. p. pygmaeus*' (1974, fig. 8) is the closest of all his figures to what is here described, and to what we believe can be detected on the syntypes of *brachycnemis* (see Remarks).

Habitat. Schiøtz (1975) describes this as a 'savanna' species, with males 'calling from grass near water in flooded fields and pools'. He reports that A. Duff-Mackay found eggs 'laid in leaf axils of grass a few inches above water'. Apparently the leaves were not glued together.

Remarks. As with so many groups of small-sized African frogs, treatment of the *brachycnemis* group has been attended by much uncertainty and confusion. The most recent published attempt to introduce taxonomic order, by Pickersgill (1984), does not throw light on *brachycnemis* itself. Schiøtz (1974) recognised two species of dwarf *Afrixalus* widespread in Malaŵi and Tanzania. The one he listed as *brachycnemis*, the other as *pygmaeus*. His statement that 'the one could easily be referred to *A. brachycnemis* (Boulenger)' is not accompanied by any discussion or description of Boulenger's syntypes, and in fact the syntypes show so few features of diagnostic value that the referral of any species to Boulenger's *brachycnemis* is far from 'easy'.

There are three syntypes of *brachycnemis*, BM 1947.2.9.77–79. There are no males in the series: 77 and 78 are females, and 79 is an 18 mm juvenile. Consequently skin asperities (used by Schiøtz as a diagnostic feature) are lacking. The patterning is faded, but syntype 77 appears to have two paravertebral bands commencing in the occipital area and broadening posteriorly, and there are faint indications of a patch on each tibia which continue the paravertebral bands when the legs are folded. Syntype 78 has faint indications of a patch on the head, a pair of faint paravertebral bands, and a faint patch over the medial surface of each tibia where, in the folded position, it would join the paravertebral band. In 79 there are faint indications of paravertebral bands meeting between the eyes in a dark patch.

Tibial markings are faded. If Schiøtz's (1974) figures of *'brachycnemis'* and *'pygmaeus'* are compared with the *brachycnemis* syntypes, his fig. 8 (of *A. p. pygmaeus*) shows the best match in its possession of a head patch and tibial patches abutting on to the broadened posterior ends of the paravertebral bands.

In his 1975 study, Schiøtz introduced other characters: a measure of 'snout' against 'horizontal diameter of eye', 'interorbital space' against 'upper eyelid', and webbing. The aged state of the *brachycnemis* syntypes militates against accurate measurement, but taking 'snout' to be the distance between the snout tip and the eye, this measure when divided by the horizontal diameter of the eye gives 82 % in 77, 94 % in 78 and 96 % in 79. These values do not have any critical bearing on Schiøtz's description of his *brachycnemis* ('snout equal to horizontal diameter of the eye') vis-à-vis his *pygmaeus* description ('snout equal to or a little longer than horizontal diameter of eye'). Regarding Schiøtz's (1975) second character, an accurate interorbital space: upper eyelid ratio is hardly attainable owing to the indefinite boundary between the two features. The width eyelid/interorbit distance values in the syntypes appear to be 60 % in 77, 59 % in 78 and 82 % in 79, which match neither 'interorbital space equal to upper eyelid' for Schiøtz's *brachycnemis*, nor 'interorbital space equal to or a little broader than upper eyelid' for his *pygmaeus*. The described difference in webbing of the fifth toe between his *brachycnemis* and *pygmaeus* ('$\frac{2}{3}$ joint free' against '$\frac{1}{2}$ joint free') does not allow a definite referral of the syntypes to either: in the syntypes the margin of the webbing reaches the disc of toe 5, and the level of the broad webbing between toes 5 and 4 shows some variation.

This review suggests that there is a lack of decisive data for matching either of the two dwarf species characterised by Schiøtz with the *brachycnemis* syntypes; the only set of features where there is some definiteness, namely the dorsal markings, appears to favour the reverse choice to the one made by Schiøtz. The indicated choice has the undesirable effect of keeping the nomenclature in a state of instability, but hopefully this will stimulate effort to gain more decisive data in southern Malaŵi, the area of the type locality. In the mean time, it seems inadvisable to provide a name for the species (if there is indeed only one and not more) which we believe was incorrectly called *brachycnemis* by Schiøtz.

Distribution. According to present taxonomic reckoning, Malaŵi to coastal Kenya.

Localities. Positively identified material from MALAŴI: Cape Maclear (BM), Chiradzulu (BM), Chitala River (MCZ), Cholo Mountain (NMZB), Limphasa Dambo (NMZB), Lujeri (NMZB), Mount Mulanje (ZMC), Nkhata Bay (NMZB), Nkazi River (MCZ).

Afrixalus delicatus Pickersgill

Afrixalus brachynemis brachycnemis (not Boulenger); Poynton 1964*a* (part):180, Stewart 1967 (part):128.
Afrixalus brachycnemis (not Boulenger); Schiøtz 1974 (part):13 & 1975 (part):89.
Afrixalus pygmaeus pygmaeus (not Ahl); Schiøtz 1974:15 & 1975 (part): 89.
Afrixalus delicatus Pickersgill, 1984:211. St. Lucia Village, Natal, South Africa. Holotype in the British Museum (N.H.), London.

Diagnosis and description (see remarks under genus). Body length not exceeding 23 mm. Minute asperities tending to cover dorsal and ventral surface in males, more restricted (ultimately to head or absent) in females. A dark canthal and dorsolateral band (occasionally with light speckling) present, not (or only slightly) extending on to the upper eyelid. Dorsal pattern, when most complete, an outline of an interocular-occipital patch, from which diverge parallel paravertebral stripes, which diverge again in the sacral area and join the dorsolateral bands if they extend that far. This pattern is only rarely complete: it is fragmented to a greater or lesser extent and may be lacking in females. A broken mid-dorsal line or series of dots is sometimes present. An oblique band on the tibia continues the dorsolateral/ paravertebral band when the leg is folded. This band also shows degrees of fragmentation.

Habitat. Pickersgill (1984) states that '*delicatus* appears to be confined to tropical and subtropical coastal bush and grassland', but that it is 'equally common in swamps, marshes and mangrove and *Hibiscus* swamp forests'. Eggs were reported to be 'deposited in leaves of vegetation just under the surface of the water, and the leaves were then folded lengthwise and glued with albumen'.

Remarks. In the covering of asperities and in markings, *delicatus* resembles *brachycnemis* as we understand it (*pygmaeus* of Schiøtz). Pickersgill states that *delicatus* differs from this form 'in dorsal and tibial patterns and breeding habits'. Paratypes with well-developed markings, such as NMZB 21974 from Dondo, differ from what we take to be the *brachycnemis* pattern only in that the posterior broadening of the paravertebral stripes is not marked. Schiøtz had previously identified such material as *pygmaeus*.

Distribution. Coastal lowlands from Durban, Natal, to the Zambesi Basin.

Localities. (Based on Pickersgill 1984), MOZAMBIQUE. Beira (NMZB), Chinizuia (NMZB), Dondo & 10 km NE (NMZB), Fambani River (BM), Inhaca Island (NMZB), Macuti (NMZB), Pungwe River Bridge (NM).

Afrixalus sp.

Afrixalus brachycnemis (not Boulenger); Schiøtz 1974 (part: Malaŵi material) 13 & 1975:84.

Diagnosis and description (see remarks under genus). Body length not exceeding 27 mm. Dorsal asperities present at least on head in males, may cover whole upper surface in males but not present on venter. Markings tend to be faintly shown: a dark canthal and dorsolateral band (usually with light speckling) present, including a posterior portion of the upper eyelid. Dorsal pattern, when most complete, a pair of dark paravertebral stripes, continuous from interocular area to urostyle tip, not substantially broadening posteriorly, not joining the dorsolateral band (which tends to fade completely in the sacral area), and not continued by a tibial band when the legs are folded. These paravertebral stripes tend to converge anteriorly and posteriorly. No dark patch on the head. Tibial markings composed of longitudinally arranged stripes. Schiøtz's figure of '*A. brachycnemis*' (1974 fig. 6) is the pattern here described.

Habitat. Schiøtz (1975) described the habitat as 'dense savanna and open farmbush', and records that 'males call from grass a few inches above water in flooded fields'.

Remarks. This 'species' could be a wastebasket category, including any dwarf

Afrixalus with longitudinal stripes only, or otherwise with no discernible markings. It is discussed under *A. brachycnemis*, with which we believe it has been confused. Unclear relationships with *A. crotalus* are discussed under that species.

Distribution. Zambia, Malaŵi, eastern Tanzania and Kenya.

Localities. Positively identified material from: ZAMBIA. Kachalola (AMNH, ZMC). MALAŴI. Deep Bay (USNM), Karonga (USNM), Limbe (AMNH).

Afrixalus crotalus Pickersgill

Afrixalus brachycnemis brachycnemis (not Boulenger); Loveridge 1953*a* (part):216, Poynton 1964*a* (part):180.
Afrixalus brachycnemis (not Boulenger); Schiøtz 1974 (part):13, 1975 (part):84.
Afrixalus crotalus Pickersgill, 1984:209. Ngorima Reserve, Zimbabwe. Holotype in the Natural History Museum of Zimbabwe, Bulawayo.

Diagnosis and description (see remarks under genus). Body size not exceeding 24 mm. Minute dorsal asperities on head only. A dark canthal and dorsolateral band (usually with light speckling) present, including posterior half of the upper eyelid. Dorsal pattern either or both (1) a mid-dorsal line extending from between eyes to urostyle tip, usually broken in places, and (2) a pair of paravertebral stripes which may converge anteriorly to join the line on the head, and which may diverge posteriorly to join the dorsolateral bands. The mid-dorsal line may expand into a stripe or narrow patch over the head. Tibia with an oblique transverse stripe or band which usually does not span the entire dorsal surface of the tibia, continuing the paravertebral or dorsolateral stripe when the leg is folded. These markings, especially in females, may be weakly or not shown.

Habitat. Reported by Pickersgill (1984) to be abundant 'on flood plains and semi-permanent pans in savanna and savanna-bush mosaic'. Pickersgill reports A. J. Lambiris as having found eggs 'laid in folded, glued leaves of vegetation at, and just under, the surface of standing water'.

Remarks. Pickersgill (1984) reports that the structure of the call of *crotalus* from Mutare is 'virtually identical' to the call of individuals from Kachalola, here referred to *Afrixalus* sp. He remarks that 'collection of material from intervening areas ought to show some link between the two'. Currently, the two forms are distinguished by the mid-dorsal line in *crotalus* and its oblique tibial marking. These features are, however, missing in some material from Zimbabwe identified by Pickersgill as *crotalus*, and more material is needed to clarify the taxonomic picture.

Distribution. Eastern Zimbabwe, central and northern Mozambique, southern Malaŵi lowlands.

Localities. (Based on Pickersgill 1984.) MALAŴI. Chikwawa (MCZ). MOZAMBIQUE. Amatongas (NMZB), Beira (NMZB), Caia (BM), Gondola–Inchope (NM), Cavalo (NMZB), Chinizuia (NMZB), Espungaberra (NMZB), Garuso (NMZB), Guro (NMZB), Inchope (NMZB), Inhamitanga (NMZB), Lower Revue Bridge (NMZB), Machipanda (NM), Magasso (NMZB), Mossuril (NMZB), Tete (NM), Vila Franco do Save (NMZB), Vila Gouveia (NMZB), Vila Manica (NMZB), Xiluvo (NMZB). ZIMBABWE. Bikita (NMZB), Chipinge (NMZB), Chiredzi (NMZB), Lundi River Bridge (NM), Machinawa Pan (NMZB), Marhumbini (NMZB), Mubangwashe (NMZB), Mutare (NM, NMZB), Mutoko (NMZB), Ngorima Reserve (NMZB), Odzi (NMZB), Pungwe Bridge (NM, NMZB), Pungwe Gorge (NMZB), Sabi Drift (NMZB), Sabi/Lundi confluence (NMZB), Stapleford (NMZB), Tsungwesi (NMZB).

Afrixalus aureus Pickersgill

Afrixalus brachycnemis brachycnemis (not Boulenger); Poynton 1964*a* (part):180.
Afrixalus aureus Pickersgill, 1984:206. Mhlatuze River valley 6 km north of Eshowe, Natal, South Africa. Holotype in the British Museum (N. H.), London.

Diagnosis and description (see remarks under genus). Body length not exceeding 26 mm. Minute asperities usually abundant over dorsum in males, restricted (ultimately to head) or absent in females; no ventral asperities. A dark canthal and dorsolateral band (usually with light speckling) present, including outer margin of the upper eyelid. Dorsal pattern poorly developed; an irregularly defined dark interorbital-occipital patch, and/or an irregular patch in the lumber region may be present. A large, irregularly shaped patch or a transverse to oblique band is usually present on the tibia, continuing the dorsolateral band when the leg is folded.

Habitat. Pickersgill (1984) observed *aureus* 'to be confined to bushveld and fairly dry grassland, breeding in ephemeral pans and cattle-watering dams'. Eggs were found 'enveloped in vertically folded, glued blades of grass about 4–6 cm above the surface of standing water'.

Remarks. The closest similarities between this relatively robust form and other forms of dwarf *Afrixalus* seem to lie to the south: most features of *aureus* recall more northern material of *knysnae* from Natal. The tibial stripes are generally smaller in *knysnae* (although they may be lacking in both forms), and *knysnae* shows a better development of asperities.

Distribution. More inland areas of Natal from Eshowe, through Swaziland to the eastern Transvaal and southern Mozambique.

Localities. MOZAMBIQUE. Estatuane (NMZB), Maputo (NM), Ponte do Calichane (NM), Zavora (NMZB).

Afrixalus wittei (Laurent)

Megalixalus wittei Laurent, 1941:127. Lukafu, Shaba, Zaïre. Holotype in the Musée Royal de l'Afrique Centrale, Tervuren.
Afrixalus wittei; Broadley 1971:120, Schiøtz 1974:12 & 1975:79.

Diagnosis and description. Body length up to 33 mm (usual size in Zambia 25–27 mm). Minute asperities scattered over dorsal surface of males, less densely scattered in females; a few ventral asperities in both sexes. A dark canthal and dorsolateral band (without light speckling) present, including at most the posterior margin of the upper eyelid. Dorsal pattern a well-marked pair of dark paravertebral bands meeting over the head, the markings tapering to a sharp point anterior to the eyes; converging towards the urostyle tip and not joining the dorsolateral bands. A dark band along the lateral surfaces of the tibia, but no distinct dorsal markings on the tibia.

Habitat. No information, apart from the species occurring in savanna.

Remarks. The constant markings of this species contrast sharply with the variability shown by the species listed above, and also with variability in markings shown by the more closely related *A. osorioi* (Laurent 1982, fig. 17). The species has recently been discussed in some detail by Laurent (1982).

Distribution. Northern Angola, southern Zaïre, south-western Tanzania, northern and north-western Zambia.

Localities. ZAMBIA. Chianga (NMZB), Kalabo (NMZB), Kalomo (NMZB), Mayau River (AMNH), Mporokoso (PEM), Salujinga (AMNH).

Afrixalus fornasinii (Bianconi)

Euchnemis fornasinii Bianconi, 1849:107. Mozambique. Type not traced.

Hyperolius bivittatus Peters, 1854:627. Boror, Mozambique. Holotype in the Zoologisches Museum, Berlin.

Hyperolius fornasinii; Günther 1858:87 & 1864:307.

Megalixalus fornasinii; Boulenger 1882:130 & 1910:531, Peters 1882:160, Hewitt 1911:224, Parker 1930:900, Cott 1932:474.

Afrixalus fornasinii fornasinii; Loveridge 1953*a*:345 & 1953*b*:145, Poynton 1964*a*:183 & 1964*b*:216 & 1966:30, Stewart 1967:130, Stevens 1974:10.

Afrixalus fornasini; Schiøtz 1974:12 & 1975:81.

Diagnosis and description. Body length up to 41 mm (adults over 28 mm). Asperities visible to naked eye over dorsal surface of both sexes, usually accentuated in areas of dark coloration by light surrounds. A dark canthal and dorsolateral band present, without light speckling apart from around asperities, including at most the margin of the upper eyelid. Dorsal pattern a broad, mid-dorsal band, tapering to a point between the eyes, and not joining the dorsolateral bands posteriorly. The ground colour to either side of the band varies according to incident light: in bright light the area is silvery, but in darkness the ground colour barely differs from the shade of the mid-dorsal and dorsolateral bands. Dark lateral banding is present on the tibiae, but there is no dorsal tibial marking.

Habitat. Reeded ponds and swamps in bush or savanna areas, frequently making use of banana axils when hibernating. Eggs deposited in folded leaves above water-level.

Remarks. The date of Bianconi's first description of this species (? terminating in a single -*i*) still needs some investigation (D. E. van Dijk, pers. comm.).

Distribution. Lowlands from south of Durban, Natal, to Kenya, including Malaŵi and eastern Zimbabwe.

Localities. MALAŴI. Chikwawa (TM), Chiromo (BM), Kondowe–Karonga (BM), Limphasa Dambo (NMZB), Lujeri (NMZB), Nyika Plateau (BM), Palm Beach (TM), Thyolo (TM). Gande; Kausi Village; Lake Malombe; Monkey Bay; Mtimbuka; Mpatamanga Gorge; Nsanje; Thyolo Mountain (Loveridge 1953*a*). Karonga; Livingstonia; Nkhata Bay (Stewart 1967). Mulanje (Schiøtz 1975). MOZAMBIQUE. Amatongas (NM), Beira (NM), Boror (ZMB), Caia (BM), Cavalo (NMZB), Chapala (NMZB), Charre (BM), Dondo (NMZB), Espungaberra (NMZB), Fambani River (BM), Garuso (NMZB), Inchope (NMZB), Lower Pungwe Bridge (NM), Macuti (NMZB), Maforga (NMZB), Manga (NMZB), Maputo (BM, NM), Morrumbala (NMZB), Nampula (NMZB), Nicaudala (NMZB), Panda (TM), Upper Pungwe Bridge (NMZB), Vila Bocage (NMZB), 10 km SSE Vila Gouveia (NMZB), Xiluvo (NMZB), Zavora (TM), Zinave (NMZB), ZIMBABWE. Bomponi (NMZB), Mutare (NMZB), Ngorima Reserve (NMZB), Nyamakari (NMZB), Stapleford (NMZB).

Genus *Hyperolius* Rapp

Hyperolius Rapp, 1842:289. Type by monotypy: *Hyperolius horstockii* (Schlegel) (Dubois, 1981). Liem 1970:110. Dubois 1981:264, Drewes 1984:50.
Crumenifera Cope, 1863:343. Type by monotypy: *Crumenifera pusilla* Cope, 1863.
Rappia Günther, 1864:130. (Substitute name for *Hyperolius* Rapp, thought to be preoccupied by *Uperolia* Gray).

Reed frogs, sedge frogs, water-lily frogs, tree frogs (part—this name is not literally applicable to the majority of species in the southern third of Africa, which inhabit open reeded swamps and pans). Pupil horizontal to round. No vomerine teeth. Omosternum moderately forked posteriorly. Fingers and toes webbed, with discs. Great variation shown in coloration and patterning, including sexual dichromatism and pattern change with age.

Males with a well-developed, round to oval gular gland.

Africa south of the Sahara, excluding the South African plateau and western plateau slopes. Eggs of most known species are laid in gelatinous masses attached to submerged vegetation, but several species are known to deposit egg masses above water-level. Water conservation in *Hyperolius*, particularly in *H. nasutus* (? including *H. benguellensis*), has been discussed by J. Loveridge (1976) and by Withers, Louw & Nicolson (1982). The available meagre data suggest that individuals spend at least a part of the dry season under loose bark (Raw 1982) and other sheltered sites (Dudley 1978) away from water.

This genus, as presently recognised, contains more species and seemingly greater biological diversity than other genera listed in this study. Yet any attempt to propose formal subdivisions seems premature: a clear picture may only emerge when comprehensive serological, karyological and other sets of data become available. The arrangement of the various species in this study is not intended to suggest a definite subdivision of the genus.

Synopsis of the Zambesiaca *Hyperolius*

Refer to comments on keys in the Introduction.

A. Adult size exceeding body length (snout to urostyle tip) of 24 mm: **tuberilinguis, platyceps major, pictus, kivuensis, q. quinquevittatus, kachalolae, argus, puncticulatus, bocagei, marmoratus.**

Adult body length less than 24 mm: **quinquevittatus mertensi, spinigularis, pusillus, viridis, nasutus, benguellensis, parkeri.**

Note: **mitchelli** has a range 21–26 mm.

B. Tibia length at least half the body length: **tuberilinguis, platyceps major, argus, pusillus, viridis, nasutus, benguellensis, parkeri, bocagei, marmoratus.**

Tibia length less than half body length: **pictus, kivuensis, q. quinquevittatus, q. mertensi, spinigularis.**

Note: **kachalolae, puncticulatus** and **mitchelli** span both groups.

C. Head width/body length more than 31 %: **tuberilinguis, platyceps major, pictus, kachalolae, argus, puncticulatus, mitchelli, spinigularis, pusillus, viridis, bocagei, marmoratus.**

Head width/body length less than 31 %: **nasutus, benguellensis.**

Note: **kivuensis, q. quinquevittatus, q. mertensi** and **parkeri** span both groups.

Hyperolius tuberilinguis Smith

Hyperolius tuberilinguis Smith, 1849 app.:26. 'Country to the eastward of the Cape Colony.' No discoverable type material. Poynton 1964*a*:189 & 1964*b*:218 & 1966:31, Stewart 1967:140, Stevens 1974:10, Schiøtz 1975:119.

Hyperolius salinae Bianconi, 1850:194. Inhambane, Mozambique. Peters 1882:169.

Hyperolius modestus Günther, 1864:307 (not Günther 1858).

Hyperolius concolor (not Hallowell); Peters 1882:164, Parker 1930:902.

Rappia sansibarica Pfeffer, 1893:97. Zanzibar. Type destroyed.

Hyperolius mossambicus Parker, 1930:904. Fambani River, Mozambique. Holotype in the British Museum, London. Cott 1932:479.

Hyperolius kivuensis smaragdinus Laurent, 1947:292. Charre, Mozambique. Holotype in the British Museum, London.

Hyperolius concolor tuberilinguis; Loveridge, 1953*a*:354 & 1953*b*:146.

Diagnosis. Size of breeding males about 27–33 mm. Canthus straight, snout fairly sharply pointed, head width/body length more than 33 %. Tibia length not less than half distance from nostril to urostyle tip. Main part of webbing level (or very nearly level) with middle subarticular tubercle of fourth toe on both sides; joining fourth toe at or just short of distal tubercle at least on outer side, continuing as a narrow margin to disc.

Description. Adult males and females usually a uniform green, less often straw-coloured. Juveniles and some breeding males brown with an hourglass pattern over the anterior part of the back and sometimes a sacral saddle. A conspicuous light canthal line continuing along the edge of the upper eyelid in juveniles, but usually disappearing in adults.

Habitat. Common in reedbeds bordering swamps and rivers. Males tend to call from reeds or stout sedges well above water-level. Eggs are enclosed in a clear gelatinous cake attached to reed or grass stems above water-level.

Distribution. Eastern lowlands from Kenya to southern Natal.

Localities. MALAŴI. Chikwawa (TM), Limphasa Dambo (NMZB), Lujeri (NMZB), Makoka A.R.S. (BM), Mangochi (NMZB), Nkwadzi Hill Forest (NMZB), Palm Beach (TM), Thyolo Mountain (NMZB). Chiromo; Mtimbuka; Nchalu (Loveridge 1953*a*), Nkhata Bay (Stewart 1967). MOZAMBIQUE. Amatongas (NM, NMZB), Beira (BM, NM, NMZB), 16 km NE Beira (NMZB), Caia (BM), Chapala (NMZB), Charre (BM), Chimonzo (TM), Chiniziua (NMZB), Dondo (NMZB), 16 km NE Dondo (NMZB), Dondo Forest (TM), Estatuane (NMZB), Fambani River (BM), Garuso (NMZB), Inhaca Island (NMZB), 8 km E Jangamo (TM), Lower Revue River (NMZB), Maforga (NMZB), Magude (TM), Maputo (NM), Mount Meponduine (NMZB), Muda/Lamego (NMZB), Nabaunama Dam (NMZB), 8 km N Nicuadala (NMZB), Ponte do Calichane (NM), Ponte do Pungwe (NM, NMZB), Savane (NMZB), Vila Bocage (NMZB), 15 km SE Vila Franca do Save (NMZB), 10 km SSE Vila Gouveia (NMZB), Xiluvo (NMZB), Zavora (TM). ZIMBABWE. Lusitu Lagoon

(NMZB), Mare Dam (AJL), Marhumbini (NMZB), Mutare (NMZB), Ngorima Reserve (NMZB), Nyamakari River (NMZB).

Hyperolius platyceps major Laurent

Hyperolius platyceps major Laurent, 1957:6. Upemba National Park, Zaïre. Type in the Musée Royal de l'Afrique Centrale, Tervuren. Schiøtz 1975:141.

Diagnosis. Size of breeding males about 25–30 mm. Canthus slightly curved, snout obtusely pointed, head width/body length 36–41 %. Tibia length not less than half distance from nostril to urostyle tip. Main part of webbing level with, or extending further than, the middle subarticular tubercle of fourth toe on both sides; joining fourth toe at or beyond distal tubercle at least on outer side and continuing as a margin to, or almost to, disc.

Description. Head very broad, giving the 'flat head' appearance for which the species is named. Markings of two different types. (1) An hourglass pattern extending from the interocular to scapular region, with a separate or attached sacral band (very similar to the juvenile *tuberilinguis* pattern). A light triangular patch over the snout may be conspicuous. (2) A light canthal and dorsolateral band, sometimes with a more or less lighter triangular patch over the snout. In both types, light and dark patterning composed of shades of brown.

Habitat. No definite information is available. *H. p. langi* is stated by Schiøtz (1975) to be a high forest form.

Remarks. Schiøtz (1975) referred a single NMZB specimen from Isombo Stream to *p. major*, with doubt. This specimen (NMZB 1508), together with nine other specimens collected in the same area by Keith and Stjernstedt, have been compared with two paratypes of *p. major*. They agree with the paratypes very well, although the web does not reach the disc of the outer toe in all the specimens, as it does in the paratypes. In the NMZB specimen, only the web margin reaches the disc. As Schiøtz noted, it has a light triangle on the snout. Judging from the other available Zambian material, this triangle is more conspicuous in individuals with the hourglass pattern, and there are indications of this pattern on the faded NMZB specimen. It seems that the specimen can be referred to *p. major* with confidence.

Listing *major* as a subspecies of *platyceps* does not imply considered endorsement of subspecific status. As Schiøtz points out, the relationships amongst the *platyceps* group still require investigation.

Distribution. Southern Zaïre and north-western Zambia, probably also adjacent Angola.

Localities. ZAMBIA. Isombo Dambo and Stream (NMZB), Salujinga (AMNH).

Hyperolius pictus Ahl

Hyperolius pictus Ahl, 1931:301. Ngosi Crater Lake, southern Tanzania. Type apparently lost from the Zoologisches Museum, Berlin. Poynton 1964*b*:217, Stewart & Wilson 1966:303, Stewart 1967:137, Broadley 1971:121, Schiøtz, 1975:135.
Hyperolius marginatus (not Peters) Loveridge 1953*a*:348.

Diagnosis. Size of breeding males about 24–28 mm. Canthus fairly curved, snout bluntly pointed, head width/body length 32–35 %. Tibia length less than half distance from nostril to urostyle tip. Main part of webbing level with or (more usually) falling short of middle subarticular tubercle of fourth toe on inner side, joining fourth toe just before distal tubercle on outer side and continuing as a faint margin to disc.

Description. A relatively short-legged form with unusually variable markings and coloration in both sexes. Markings fall into three main types: (1) a uniformly coloured dorsum, (2) longitudinal light bands, (3) irregular longitudinal dark bands.

Habitat. Common around small pools, ponds and streams on the dambos of the Nyika Plateau. During the day, individuals sit on heaths and sedges about a metre above water-level (Stewart & Wilson 1966). Eggs laid in gelatinous clusters above water-level (Stewart 1967).

Distribution. Highlands of south-western Tanzania, northern Malaŵi and adjoining Zambia.

Localities. Chelinda (USNM), Chisenga (USNM), Nyika Plateau in Malaŵi and Zambia (AMNH, NMZB).

Hyperolius kivuensis kivuensis Ahl

Hyperolius kivuensis Ahl, 1931:280. Lake Kivu, Zaïre. Type in the Zoologisches Museum, Berlin. Laurent 1947*a*:291, Broadley 1971:121, Schiøtz 1975:115.
Hyperolius rhodoscelis (not Boulenger) Loveridge 1933:404.

Diagnosis. Size of breeding males about 27–33 mm. Canthus straight, snout pointed, head width/body length 29–34 %. Tibia length less than half distance from nostril to urostyle tip. Main part of webbing level with middle subarticular tubercle of fourth toe on both sides (rarely not quite level on inner side), joining fourth toe at distal tubercle on outer surface and continuing as a distinct margin to disc; joining fifth toe closer to disc than to distal tubercle, usually very close to disc.

Description. A relatively short-legged form; adults typically with a uniformly coloured dorsum and a dark band along canthus, continuing behind eye as a dark lateral band for a variable length. Dorsal to the band, the coloration may be lighter: in juveniles, this appears as a distinct light dorsolateral band with a dark medial border, and another dark-bordered light band is present on the midline. This juvenile pattern is hardly distinguishable from the striped pattern of adult *quinquevittatus* of the same size. As noted by Laurent (1947*a*), this could lead to these taxa being confused.

Habitat. Well-wooded moist savanna.

Remarks. Although this form has sometimes been confused with *tuberilinguis*, it is even more likely to be confused with *quinquevittatus*, which it just overlaps in size even though adults are usually bigger. Juvenile *kivuensis* have a striped pattern (Laurent 1941, pl. 9) which is very similar to the striped *quinquevittatus* adult pattern, and both species have relatively short legs and a pointed snout (but tending to be less pointed in *kivuensis*). The less extensive webbing in *quinquevittatus* (see respective diagnoses) appears to offer a reliable way of separating the two species. Using this criterion, the southern Malaŵi material identified by Schiøtz (1975) and with reservations by Stevens (1974) as *kivuensis* is referable to *q. quinquevittatus* (see Remarks under that form).

Distribution. From southern Uganda to southern Zambia.

Localities. ZAMBIA. Chambeshi River (NMZB), Chisamba Falls (NMZB), Chunga (NMZB), Kachalalo (ZMK), 16 km N Kafue River Bridge (ZMK), Kasama (ZMK), Lake Chila (BM, ZMK), Lucheche (BM), Mazabuka (ZMK), Mbala (PEM), Mpika (ZMK), Mpulungu (NMZB), Niamkolo (BM, MCZ). Mbala (Schiøtz 1975).

Hyperolius quinquevittatus quinquevittatus Bocage

Hyperolius quinquevittatus Bocage, 1866:56. Duque de Bragança, Angola. Type destroyed.
Hyperolius q. quinquevittatus; Broadley 1971:121.
Hyperolius kivuensis (not Ahl); Stevens 1974:10, Schiøtz 1975 (part):115 (Malaŵi records).

Diagnosis. Size of breeding males about 21–28 mm. Canthus straight, snout pointed, head width/body length 29–33 %. Tibia length less than half distance from nostril to urostyle tip. Main part of webbing not level with middle subarticular tubercle of fourth toe on either side, joining fourth toe at or (more usually) before distal tubercle, no distinct margin of web beyond distal tubercle; fifth toe usually completely free of web beyond distal tubercle.

Description. A small, relatively short-legged form, with two main colour patterns which are at least to some extent age-dependent, although seemingly not sex-dependent. The 'five-striped' pattern for which the species is named is well developed in juveniles and some adults: a pair of light dorsolateral bands, a light vertebral band and a pair of often less conspicuous light paravertebral bands. These are separated by dark stripes. In at least some adults the vertebral and paravertebral bands merge as the dark stripes disappear, leaving finally a more or less uniform dorsum, together with a light dorsolateral band bordered by a dark lateral stripe below and a more or less broken dark stripe above. These correspond to Pattern 1 or Pattern 2 respectively of Schiøtz (1975). The end result is a pattern very similar to *kivuensis*. There is no standard size at which the transformation takes place, at least in males.

Habitat. A savanna species. Found calling from grass stems near swampy areas (Schiøtz 1975). Taken in swampy grassland at Ikelenge (C. A. Green, field notes).

Remarks. Schiøtz (1975) suggested that an east–west cline in markings exists in this species, eastern material showing a tendency to lose the dorsal banding. He did not appear to take into account the fact that, as in *kivuensis*, the dorsal markings tend to disappear with age. This tendency is undoubtedly present in western material: in the NMZB Ikelenge (western Zambia) series of four specimens, the two largest specimens show loss of dorsal banding, as does a 25 mm female from Zambia/Angola/Shaba border. Laurent (1957) noted a similar reduction of dorsal markings with age in Upemba Park material.

Schiøtz (1975) considered *quinquevittatus* to be 'an unmistakable species. In morphology it is rather close to *H. nasutus*. . . .' But in shortness of tibia it is much more similar to *kivuensis*, which it seems to resemble closely in all other features except in its smaller size and more reduced webbing. The southern Malaŵi material identified by Schiøtz as *kivuensis* has the relatively reduced webbing of *quinquevittatus*. The specimens are adult, with a uniform dorsum apart from a trace of the light vertebral band: this is the '*kivuensis*' pattern, differing from true *kivuensis* apparently only in detail, such as a more complete dark lateral stripe reaching nearly to the groin, and a light band running the length of the tibia on its dorsolateral surface. Juvenile material collected by Stevens at Chisambo and Lambert at Makoka A.R.S. (near Zomba) shows the typical striped pattern.

Distribution. Northern Angola, southern Zaïre, northern half of Zambia, southern Tanzania, Malaŵi excluding the Nyika Plateau and the southern lowlands.

Localities. ZAMBIA. Ikelenge (NMZB), Isombo Dambo (NMZB), Kasama (ZMK), Kasempa (AMNH), Lake Chila (BM, ZMK), Lucheche (BM), Mbala (PEM, NMZL), 48 km from Ndola, Mufulira Road (AJL), Salujinga (AMNH), Zambia/Shaba/Angola border (NMZB). Isoka; Luwinga; Mufabushi River (Schiøtz 1975). MALAŴI. Mlange (ZMK), Makoka A.R.S. (BM), Zomba (BM), Zomba district (NMZB).

Hyperolius quinquevittatus mertensi Poynton

Hyperolius mertensi Poynton, 1964*b*: 220, Nyika Plateau, Zambia. Holotype in the Natural History Museum, Bulawayo. Stewart & Wilson 1966:305, Stewart 1967:146.
Hyperolius quinquevittatus mertensi; Broadley 1971:121, Schiøtz 1975:105.

Diagnosis. Size of breeding males about 18–24 mm. Canthus straight, snout obtusely pointed, head width/body length 30–34 %. Tibia length less than half distance from nostril to urostyle tip. Main part of webbing not to just level with middle subarticular tubercle of fourth toe at least on outer side, joining fourth toe at or before distal tubercle; toe without a distinct margin of web beyond this tubercle. Fifth toe free of web beyond distal tubercle.

Description. A small, relatively short-legged form, with a dark lateral band running along canthus and continuing behind eye to groin. Juveniles with a pair of broad, dark paravertebral bands with more darkened borders (see Remarks); with growth these bands disappear, leaving the lateral border as a single dorsolateral stripe before disappearing (initially at the anterior end) altogether. The background colour is green to yellow in life, becoming grey in alcohol.

Habitat. Found on short grasses and sedges in dambos, breeding in small pools between tussocks (Stewart & Wilson 1966, Stewart 1967).

Remarks. The loss of dorsal markings with age, and hence the disappearance of the '*quinquevittatus*' pattern in Nyikan material, was not fully appreciated when Poynton (1964*b*) described the material as *mertensi*. However, the striped juvenile pattern proves to differ somewhat from the juvenile pattern of true *quinquevittatus*: in *mertensi* the dark paravertebral stripes are closer to the next pair of stripes than they are in *quinquevittatus*, to the extent that they virtually merge, so that, as described by Stewart (1967: 147), 'there is a pair of broad, tan bands in the dorsolateral position. Each band looks almost double.' The paravertebral stripes become indistinct in *c*. 20 mm specimens (Stewart: 'the lateral portion of the tan bands becomes black and the median portion fades to silver'), leaving at most a line on either side of the urostyle. This is similar to the condition in mature *quinquevittatus*, although the remains of each paravertebral line are much closer to (or merging with) the next, unlike *quinquevittatus*.

It is thus possible to distinguish juvenile *mertensi* from *quinquevittatus* on this feature of the patterning: in *mertensi* the vertebral-urostylar light band is wider than the light band to either side (if this band is clear at all); in *quinquevittatus* the bands are subequal or the vertebral-urostylar band is narrower. In adults where these markings disappear, *mertensi* may be distinguished by its slightly smaller size, males not being known to exceed 24 mm, while males of *quinquevittatus* in southern Malaŵi exceed 26 mm. Schiøtz's (1975) suggestion that *mertensi* represents the eastern extreme of an east–west cline in *quinquevittatus* is not accurate, if we are correct in assigning to *quinquevittatus* the southern Malaŵi material included in *kivuensis* by Schiøtz (see Remarks under *q. quinquevittatus*).

Distribution. Nyika Plateau of Zambia and Malaŵi.

Localities. ZAMBIA. Nyika Plateau (NMZB). MALAŴI. Nyika Plateau (NMZB), Chelinda Bridge, Nyika (NMZB), Chelinda Depot (USNM).

Hyperolius kachalolae Schiøtz

Hyperolius kachalolae Schiøtz, 1975:162. Near Kachalola, Zambia. Holotype in the Zoologisk Museum, Copenhagen.

Diagnosis. Size of breeding males about 25–29 mm. Canthus more or less straight, not prominent, snout bluntly pointed, head width/body length 31–38 %. Tibia length slightly to decidedly more than half distance from nostril to urostyle tip, but less than this distance in one female. Main part of webbing level with, to just falling short of, middle subarticular tubercle of fourth toe on outer side, joining toe near or at distal tubercle on outer side and continuing as a distinct fringe.

Description. Preserved material without clear markings, although a faint canthal and dorsolateral line usually present. In life, this line consists of minute red spots, according to Schiøtz (1975), who describes the overall coloration as being green, yellow or brown, with bright turquoise blue vocal sacs in calling males. Apart from gular coloration, there appears to be no sexual dichromatism.

Remarks. Schiøtz compared *kachalolae* only with *argus*. To the extent that specimens of *kachalolae* have any markings, the pattern recalls *bocagei*, which *kachalolae* resembles in webbing and general proportions. The strong flap of the gular gland differs from the rather baggy, *marmoratus*-like flap of *bocagei*, but the possibility that *kachalolae* is an eastern population or derivative of *bocagei* deserves investigation in the field.

Distribution. Known only from Kachalola, Zambia, east of Lusaka.

Localities. ZAMBIA. Kachalola (AMNH, ZMK).

Hyperolius argus Peters

Hyperolius argus Peters, 1854:628. Boror, Mozambique. Type apparently lost. Peters 1882:164, Parker 1930:902, Cott 1932:477, Poynton 1964*a*:187 & 1964*b*:217 & 1986 p. 149, Stewart 1967:135, Stevens 1974:10, Schiøtz 1975:157.
Hyperolius flavoviridis Peters 1854:628. Boror, Mozambique. Peters 1882:163.
Hyperolius tettensis Peters 1854:628. Tete, Mozambique. Peters 1882: pl. 5.
Rappia platycephala Pfeffer, 1893:96. Quelimane, Mozambique. Type destroyed.
Hyperolius argus argus; Loveridge 1953*a*:356, Laurent 1961:74.
Hyperolius puncticulatus puncticulatus (not Pfeffer); Poynton 1964*a*:186.

Diagnosis. Size of breeding males about 27–34 mm. Canthus more or less straight, not prominent, snout bluntly pointed, head width/body length 36–42 %. Tibia length more than half distance from nostril to urostyle tip. Main part of webbing level with or passing middle subarticular tubercle of fourth toe on both sides, joining toe at distal tubercle on both sides and continuing as a distinct fringe.

Description. A large form with extensive webbing and sexual dichromatism, with much variation in markings of males. In males, light canthal and dorsolateral banding may be absent to indistinct to distinct. If present, it narrows (or disappears) over eyelid. Dorsolateral band usually about as broad as canthal band to broader (but not twice as broad), extending to groin or at least well past position of elbow. Back usually with dark speckles or dots, which are usually denser above and below the dorsolateral bands, forming a more or less definite dark edging or border.

In females, the light canthal band, if present, does not narrow over eyelid and may even broaden out, giving the impression of spectacles (although these do not circle round behind and beneath the eye). The band does not continue behind the eye, but starting behind the eye there may be a dorsolateral series of light bands or spots, regular or irregular in outline. Asymmetrically placed spots may also occur on the dorsum, but these are much less common towards the south of the range, and are quite unusual in Natal material. All light markings have a fine, unbroken black edging. No dark speckles or dots occur on the back.

In life, calling males at night are yellow, olive green, brownish or blackish above, sometimes with scattered small black spots. The skin appears translucent. The ventrum is densely pigmented white, and the vocal sacs are green. Females at night are reddish or purple with orange 'spectacles'. The dorsal spots and the limbs are bright orange.

Habitat. More or less open savannas, and larger bodies of still water, such as backwaters of big rivers, open swamps or dams especially where water-lilies are present. Males usually call from flat surfaces just above water-level, such as are provided by floating vegetation (lily pads are strongly preferred) or flat stones. Calling from reeds and bushes also occurs. During the day individuals may be found hiding in floating Nile Cabbage *(Pistia stratiotes)* or lily pads.

Remarks. There is a marked north–south cline in this species, discussed by Poynton 1986. While it may be difficult to distinguish some male *argus* from *puncticulatus*, the diagnosis under these species indicates ways of separating the two according to details of markings. In addition, webbing is less well developed in *puncticulatus*. There appears to be a definite ecological difference, *argus* breeding in bodies of open water, whereas *puncticulatus* is associated with forest. So far, sympatry has not been found in the Zambesiaca area, *puncticulatus* being known only from montane forests in Malaŵi.

It is also easy to confuse *argus* with *mitchelli*, described by Loveridge as a subspecies of *puncticulatus*. This species is sympatric with *argus* in Mozambique.

Distribution. Southern Somalia (Lanza 1981) along the coastal lowlands to Durban, South Africa.

Localities. MALAŴI. Chiromo (NMB). MOZAMBIQUE. Beira (NM), Boane (NMZB), Caia (BM), Charre (BM), Dondo (NMZB), Fambani River (BM), Grudja (NMZB), Lower Revue Bridge (NMZB), Macuti (NMZB), Maringa

(NMZB), Nova Sofala (NMZB), Ponte do Pungwe (NMZB), Zavora (TM), Zinave (NMZB). Boror; Cabaceira; Tete (Peters 1882), Quelimane (Pfeffer). ZIMBABWE. Marhumbini (NMZB), Ngorima Reserve (NMZB).

Hyperolius puncticulatus (Pfeffer)

Rappia puncticulata Pfeffer, 1893:99. 'Zanzibar'. Type destroyed.
Hyperolius p. puncticulatus; Loveridge 1953*a*:358 & 1953*b*:146.
Hyperolius p. choloensis Loveridge, 1953*a*:359. Thyolo (Cholo) Mountain, Malaŵi. Holotype in the Museum of Comparative Zoology, Harvard.
Hyperolius puncticulatus; Poynton 1964*b*:216 (part), Stewart 1967:132 (part), Stevens 1974:10, Schiøtz 1975:146.

Diagnosis. Size of breeding males 26–32 mm. Canthus more or less straight, not to fairly prominent, snout bluntly pointed, head width/body length 35–38%. Tibia length usually less, rarely more, than half distance from nostril to urostyle tip. Main part of webbing level to passing middle subarticular tubercle of fourth toe at least on outer side (occasionally falling just short), joining toe at distal tubercle on outer side (occasionally falling short) but usually falling short on inner side (occasionally joining only at level of middle tubercle) and continuing as a distinct fringe.

Description. A fairly large form with a light band on canthus, continuing as a narrower strip over upper eyelid to a dorsolateral band extending usually beyond arm insertion and continued sometimes by spots. The dorsolateral band is usually about as broad as the canthal band or slightly broader, but nowhere near twice as broad. A light mid-dorsal band or series of spots may be present, more rarely light asymmetrical dorsal spots or vermiculations (see Remarks). All light markings have a fine to broad, unbroken dorsal and ventral black edging. Back usually without dark speckling or dots in the adult, but these are present in juveniles and can persist in adults.

Habitat. This species is associated with forests. The Mugesse Forest series was collected at night along roads and paths through the forest. The frogs were sitting on leaves about one or two metres from the ground. None was calling as the rains had not yet broken. Calling appears to take place above ground or water-level, in contrast to *H. argus*: the statement in Poynton (1964*a*) that *puncticulatus* 'prefers calling on lily pads' refers to *argus*, with which it was confused.

Remarks. The type of *puncticulatus* has been destroyed, and we have not been able to locate topotypes of the species as it is conventionally understood. Pakenham (1983) reported failure to find material on Zanzibar Island, while Loveridge's (1933) single 'topotype' from Mwera, Zanzibar Island, differs from the seemingly careful drawing of Pfeffer's type and only specimen in showing a broadening of the light dorsolateral bands and conspicuous heel patches. These are features of *H. mitchelli*, although the heel marking does show some variation (p. 203). The markings of the specimen figured by Pfeffer in fact resemble the appearance of some *H. argus* males, particularly the type of marking that has become stabilized in Natal material (Poynton 1986), which raises the question of *puncticulatus* being a synonym of *argus*. The illustration and description of Pfeffer's *platycephala* suggests very strongly that the type of this species was a female *argus*, but the webbing shown in Pfeffer's figure of *puncticulatus* is less extensive than the webbing shown in *platycephala*, and the statement 'Zehen halb geheftet' in the *puncticulatus* description contrasts with the statement in the *platycephala* description, 'Zehen mit Ausnahme der grossen vierten Zehe fast ganz geheftet'. The less extensive webbing of the *puncticulatus* type specimen seems valid grounds for separating it from *argus*.

If *mitchelli* and *argus*, both coastal lowland species, differ from the type of *puncticulatus*, justification has to be given for the conventional procedure of referring to *puncticulatus* a species which, at least in the Zambesiaca area, is restricted to montane forest. Loveridge's (1936) record of *puncticulatus* from Malindi on the Kenya coast becomes relevant here: we can confirm Schiøtz's (1975) opinion that this specimen (MCZ 20701) is *puncticulatus* as we understand it, and that *puncticulatus* is not so much a montane species as a forest species. A record of *puncticulatus* from the type locality of 'Zanzibar' (either the island or the adjacent mainland) can therefore be accepted, since there is a residual forest association present on the island (Moreau & Pakenham 1940) as well as on the mainland.

As noted by Procter (1920), Pfeffer's figure of *puncticulatus* shows a mid-dorsal line in the interocular region. This could be an indication of the *choloensis* character of a band or spots in the anterior mid-dorsal region, which Schiøtz (1975) reports in material as far north as the Ulugurus. The material from Morogoro listed by Procter as *puncticulatus* is, however, *mitchelli*.

It could be argued that the very name *'puncticulatus'* casts doubt on our and Schiøtz's use of the name, since Schiøtz (1975:153) distinguishes his *puncticulatus* from *mitchelli* on the uniform dorsal ground colour of *puncticulatus*. But his own fig. 145 shows a dark-spotted *puncticulatus* from Dabaga, and he notes spotting in the juvenile phase. In Stewart's USNM material, a 24,8 mm juvenile and a 26,7 mm male from Matipa Forest show a moderate degree of dark spotting, and heavy spotting is shown on two males from Chisenga (USNM 153326, 28), recalling the *mitchelli* condition. Another 28 mm male from Chisenga has virtually no spotting. Evidently a uniform to spotted condition is included in the variation of both *puncticulatus* and *mitchelli* (p. 203).

Regarding the light markings, Schiøtz (1975) illustrated three different types of patterning, two characterising a 'northern population' and one characterising a 'southern population'. All the patterns occur in Malaŵi, and specimens from Zomba Plateau show massive dorsolateral bands which surpass the 'broad pattern' illustrated by Schiøtz in the 'northern population' (1975 fig. 144). Evidently the variation in patterning cannot be attributed to a north–south cline, and it seems worth accumulating more data than the meagre amount currently available to test whether *'puncticulatus'* as here understood does in fact include only one natural species.

Distribution. Coastal Kenya, coastal Tanzania extending into the southern highlands, highlands of Malaŵi. Schiøtz's (1975) record from Marhumbini, Zimbabwe, is based on what we consider to be *argus*, even though the webbing in this series just falls short of the discs. Poynton's (1964*a*) records for South Africa are also based on *argus* (Poynton 1986).

Localities. MALAŴI. Chikangawa (NMZB), Chisenga (USNM), Likabula River, Mulanje (MCZ), Livingstonia (USNM), Lujeri Estate (NMZB), Karonga

(USNM), Matipa Forest (BM, USNM), Misuku Hills (NMZB), Mugesse Forest, Misuku (NMZB), Nkhata Bay (USNM), Nyika Plateau (BM), Ruo Gorge, Mulanje (NMZB), near Thyolo (TM), Thyolo Mountain (MCZ), Zomba Plateau (TM). Limbe (Loveridge 1953*b*). Loveridge's single Nchenachena specimen has a tail and now has no markings: it seems unidentifiable.

Hyperolius mitchelli Loveridge

Hyperolius puncticulatus mitchelli Loveridge, 1953:360, 'almost on shore of Lake Nyasa a few miles north of Mtimbuka', Malaŵi. Holotype in the Museum of Comparative Zoology, Cambridge.
Hyperolius puncticulatus (not Pfeffer); Poynton 1964*b*:216 (part), Stewart 1967:132 (part), de Fonesca & Mertens (1979).
Hyperolius puncticulatus puncticulatus (not Pfeffer); Poynton 1964*a*:186 (part).
Hyperolius mitchelli; Schiøtz 1975:151.

Diagnosis. Size of breeding males about 21–26 mm. Canthus more or less straight, fairly prominent, snout pointed, head width/body length 34–37 %. Tibia length usually less, rarely slightly more than half distance from nostril to urostyle tip. Main part of webbing level to passing middle subarticular tubercle of fourth toe on outer side, level with tubercle on inner side, joining toe at or just short of distal tubercle on both sides, and continuing as a narrow fringe.

Description. A fairly small-sized form with a light band on canthus, continuing as a narrower strip over upper eyelid to a dorsolateral band that ends near groin, or at least well behind the position of the elbow. Dorsolateral band noticeably broader than canthal band, typically not far from being twice as broad. Light cantho-lateral bands usually with a definite, unbroken dark edging, sometimes lacking to almost lacking in the posterior half of the body. A light patch or spot on the heel usually present. Upper surface of body and limbs usually with a scattering of a few to several dark spots, but these may be absent. The pattern is the same in adults of both sexes.

Habitat. The Maforga specimens were calling from shrubs beside a small marshy stream in an area of evergreen forest savanna mosaic. Schiøtz (1975) noted an association of this species with forest, and found it sharing the same calling site with *puncticulatus* at Amani in Tanzania. De Fonesca & Mertens (1979) found this species in dense reed and report that the egg cluster is deposited on a leaf overhanging water.

Remarks. Loveridge (1953*a*) described his *puncticulatus mitchelli* as 'slightly resembling *H. p. substriatus* Ahl'. But MCZ 17162 from Mwera, Zanzibar, thought by Loveridge (1933) to be a topotype of *puncticulatus* Pfeffer, and subsequently referred by him (1953*a*) to *substriatus*, appears to be *mitchelli*. It is a 25,7 mm female with half-developed eggs, and there is a large light patch on each heel, as well as the typical broadening of the dorsolateral band. In size and light markings it therefore agrees with *mitchelli*. It lacks dark spots on the upper surfaces, but this falls within the range of variation of *mitchelli*: in the eleven specimens of the Maforga series, for example, dark speckling is sparse to absent, and it is also absent on the two paratypes, as noted by Loveridge.

Possibly because of this lack of spotting, Schiøtz (1975) remarked that the *mitchelli* paratypes 'may equally well be *H. puncticulatus*'. The largest specimen

(MCZ 27273) is a mature male only 25,3 mm in length, and the dorsolateral band broadens over the body and reaches almost to the groin. These features place it in *mitchelli* rather than *puncticulatus*, even though there is no sign of dorsal speckling or a spot on the heel. In the smaller paratype, all markings are very indistinct.

The smallness or even lack of the light heel mark in southern material may indicate a north–south cline in this feature. Be this as it may, variation in this heel mark and in dorsal dark spots makes it necessary to withdraw these two characters from the few listed by Schiøtz as separating *mitchelli* from *puncticulatus*. To the list could be added the tendency in *mitchelli* for the dorsolateral band to broaden between scapula and sacrum (shown very well in Schiøtz's fig. 149), a feature not shown in *puncticulatus* (cf. Schiøtz figs 144–145).

So far, Schiøtz's experience of finding these two very similar species 'sympatric in the strictest sense' at Amani, Tanzania, has not been paralleled in the Zambesiaca area. While resemblance between the patterning of southern *mitchelli* and some individuals of *argus* is strong, the two species can be told apart by the fuller webbing and appreciably greater size of *argus*.

Distribution. North-eastern Tanzania to Mozambique.

Localities. MALAŴI. Mtimbuka (MCZ), Nkhata Bay (NMZB, USNM). Katendeza; Kawiya Mouth (de Fonesca & Mertens 1979). MOZAMBIQUE. Chiniziua District (NMZB), Maforga (NMZB).

Hyperolius spinigularis Stevens

Hyperolius spinigularis Stevens, 1971:313. Chisambo Tea Estate, Mulanje, Malaŵi. Holotype in the Natural History Museum of Zimbabwe, Bulawayo. Stevens 1974:10, Schiøtz 1975:165.

Diagnosis. Size of breeding males about 18–24 mm. Canthus more or less straight, not very prominent, snout bluntly pointed, head width/body length 34–36 %. Tibia length less than half distance from nostril to urostyle tip. Main part of webbing level with middle subarticular tubercle of fourth toe on both sides, reaching, to not quite reaching, distal tubercle, and continuing to disc as a narrow fringe.

Description. Males small in size, averaging about 21 mm, but females larger, averaging about 28 mm. Breeding males with black asperities on the bilobed gular gland, ventrum and undersurface of hind limbs. Females without ventral asperities, but minute asperities usually present on dorsal surface of both sexes, although less developed in females. No sexual dichromatism; pattern ranging from a regular cantho-dorsolateral light band to extensions of the band to produce a light triangular frontal patch and light blotching on the back. Heel spots present or absent.

Habitat. 'The species prefers rather overgrown dambo areas in protected situations' (Stevens 1971). Schiøtz (1975) collected material 'on the edge of Amani Pond, an artificial lake in rather dense forest'. Eggs are laid 'in a single mass amongst grass stems or on the underside of leaves just above water level on the edge of the pool or stream' (Stevens 1971). Stevens observed one female returning to the egg mass on the two consecutive nights after laying it and 'ejecting a watery fluid over the egg mass from her vent'.

Neither Stevens nor Schiøtz heard males of this species calling in the field.

Distribution. Known only from Mulanje, Malaŵi, and Usambara Mountain, Tanzania (Schiøtz 1981).

Localities. MALAŴI. Chisambo (BM, NMZB), Ruo Estate (Stevens 1971).

Hyperolius pusillus (Cope)

Crumenifera pusilla Cope, 1862:343. Umvoti, Natal. Holotype in the Academy of Natural Sciences, Philadelphia.

Hyperolius microps Günther, 1864:311. Rovuma Bay, Tanzania. Syntypes in the British Museum, London. Parker 1930:905, Cott 1932:479.

Hyperolius pusillus; Loveridge 1953*b*:147, Poynton 1964*a*:191 & 1964*b*:218 (part), Stewart 1967:142, Stevens 1974:10. Schiøtz 1975:105 Dudley 1978:91.

Diagnosis. Size of breeding males about 17–21 mm. Canthus curved, snout tending to be truncated, head width/body length 34–39 %. Tibia length more than half distance from nostril to urostyle tip. Main part of webbing level with or passing middle tubercle of fourth toe on outer side, just passing to not quite reaching tubercle on inner side, joining toe at distal tubercle at least on outer side, but continuing only as a very narrow fringe if at all.

Description. A small-sized species, a translucent green in life but becoming cream-coloured when preserved. A dark canthal line usually present, dorsal surface immaculate to quite densely covered with dark spots, sometimes arranged to form the outline of an inverted triangle over the occipital area, which may continue as a mid-dorsal line.

Habitat. Open savanna pans are preferred. Males are typically found calling on lily pads, and antiphonal calling bouts can develop between a male of this species and the much larger *argus* on the same pad. Eggs are laid between overlapping lily leaves.

Remarks. Schiøtz (1975) reported that his material from the dry parts of Kenya differed from 'typical' *pusillus* in being somewhat larger (males 20–22 mm) and in having the dorsal spots arranged in a triangular or hourglass pattern. He noted that taxonomic separation may be indicated. A series of nine NMZB males from Malugwe Pan, in a drier part of eastern Zimbabwe, compares with Schiøtz's Kenya material both in size (20,7–22,7 mm), and in markings in that one of the specimens has dark spots arranged to form an occipital triangle. This variation would have to be taken into account if taxonomic separation of Kenyan material is to be proposed.

The Zambian records of *pusillus* in Poynton (1964*b*) are based on specimens of *viridis* Schiøtz, treated below.

Distribution. Lowlands from southern Somalia (Lanza 1981) to Transkei.

Localities. MALAŴI. Fisheries Station, L. Chilwa (JV). Chiromo (Loveridge 1953*b*), Kambwe (Stewart 1967). MOZAMBIQUE. Beira (NMZB), Boane (BM), Dondo (NMZB), Estatuane (NMZB), Fambani River (BM), Macuti (NMZB), Mount Meponduine (NMZB), Nova Lusitania (TM), Pomene (TM), Ponte do Calichane (NM), 3,5 km S Siteki (TM), Xiluvo (NMZB), Zavora (TM), Zinave (NMZB), ZIMBABWE. Chipinda Pools (NMZB), Malugwe Pan (NMZB), Naivasha Pan (NMZB), Nyala Pan (NMZB).

Hyperolius viridis Schiøtz

Hyperolius viridis Schiøtz 1975:110. '30 miles southwest of Mbeya, Tanzania.' Holotype in the Zoologisk Museum, Copenhagen.
Hyperolius pusillus (not Cope); Poynton 1964*b*:218 (part: Chipangali & Mkanda).

Diagnosis. Size of breeding males about 21 mm. Canthus curved, snout tending to be truncated, head width/body length about 33 %. Tibia length more than half distance from nostril to urostyle tip. Main part of webbing not reaching middle subarticular tubercle on either side, almost or just reaching distal tubercle on outer side and continuing as a distinct margin.

Description. A small-sized species, very similar to *pusillus* in appearance, but differing in the more reduced webbing and the possession (usually) of a light dorsolateral pair of lines at least in males. This latter feature could lead to confusion with *nasutus*. A 21,3 mm NMZL female from Isoka has no dorsolateral lines or rows of spots. Dorsal surface virtually immaculate to densely covered with dark spots.

Habitat. Differing markedly from the morphologically very similar *pusillus*: Schiøtz (1975) records that the calling site of *viridis* is grass. This could lead to confusion with the not too different *nasutus*.

Distribution. Southern Tanzanian and eastern Zambian highlands. It should be looked for in western Malaŵi.

Localities. ZAMBIA. Chipangali (NMZB), Isoka (NMZL), Mkanda (NMZB).

Hyperolius nasutus Günther

Hyperolius nasutus Günther, 1864*b*:482. Duque de Bragança, Angola. Holotype in the British Museum, London. Loveridge 1953*a*:362, FitzSimons 1958:212, Broadley 1971:121, Stevens 1974:10, Schiøtz 1975:97, J. Loveridge 1976:325 (? includes *H. benguellensis*).
Rappia nasuta (Boulenger); Hewitt, 1911:224, Hewitt & Power 1913:170.
Hyperolius granulatus (not Boulenger); Loveridge 1933:410.
Hyperolius nasutus nasutus; Poynton 1964*a*:192 & 1964*b*:219 & 1966:31 & 1982:70, Stewart & Wilson 1966:304, Stewart 1967:144.
Hyperolius sp. FitzSimons 1939:44.

Diagnosis. Size of breeding males about 19–22 mm. Canthus straight, snout elongated and pointed, projecting well beyond mouth and somewhat shark-like in side profile; head width–body length 27–31 %. Tibia length usually more than half distance from nostril to urostyle tip, rarely equal to half. Main part of webbing level with middle subarticular tubercle of fourth toe on both sides, to falling short on inner side, usually reaching distal tubercle on both sides but occasionally not reaching it on inner side, continuing as a very thin fringe; joining the third toe anywhere from disc to distal subarticular tubercle.

Description. A small-sized species characterised by a pointed snout, shark-like in profile. Head and body very long and slender. Coloration a general translucent green in life, becoming straw-coloured when preserved. A light dorsolateral band generally present in males, less common in females, present as an unspotted belt or accentuated by white pigment. Immaculate above to densely covered with fine to coarse dark dots, the dots characteristically concentrated to form a mid-dorsal line, sometimes also formed into dorsolateral and lateral series.

Habitat. Males call from grass stems, sedges and reeds, well above water-level. This is typically an open savanna or grassland species.

Remarks. Material that could be interpreted as belonging to a different species, very similar to *nasutus* but occurring in more upland and western areas, is discussed as *H. benguellensis* (formerly *H. granulatus*) below. There appears to be intergrading between *nasutus* and that species (Poynton 1982). Variation in markings and the degree of webbing in *nasutus* is discussed under *benguellensis*.

In southern material, namely some Caprivi and (more notably) southern Mozambique and Natal specimens, males tend to have the dorsolateral band markedly whitened. This feature is lacking or only weakly shown in more northern adult males in the Zambesiaca area, and a white band is lacking in females. There is thus a well-marked sexual dichromatism in southern material. Schiøtz (1975) records considerable geographical variation in size, shape of snout and in markings, which we can confirm. In some populations, Schiøtz notes that only males have light dorsolateral banding, but in other populations, both sexes are recorded as having these bands. Schiøtz observes (1975:100): 'I have not been able to find any geographical sense in the distribution of these characters.' The marked white banding of southern males is the only geographical pattern to the variation that we have discerned.

Distribution. See Poynton 1982, fig. 5. 'Typical' *nasutus* occurs in the Natal coastal region, Mozambique, Malaŵi, eastern Zambia, and tropical savannas northwards and westwards. 'Typical' *nasutus*, but also apparent hybrids with *benguellensis*, occur in Zimbabwe, Botswana, Caprivi, western Zambia, Namibia, Angola and Zaïre.

Localities. BOTSWANA. Boro River (TM), Boro/Kiri Confluence (TM), Chobe (TM), Four Rivers Camp (NMZB), Gugathebe Bridge (TM), Kasana (NMZB), Kiri River (TM), Maun (NMZB), 16 km SW Maun (NMZB), Maxwee (NMZB), Mboma (NMZB), Piajo (TM), Pom Pom (NMZB), Xaxaba (NMZB). CAPRIVI. Kwando River (TM), Linyanti (TM), Old Sangwali (TM), Schuckmansburg (TM). ZAMBIA. Chibodio Dam (BM), Chila (BM), Chilonoma (BM), Chipangali (NMZB), Chunga N.P. (NMZB), Isoka (BM, NMZL), Isombu (NMZB), Kalabo (FMNH), 40 km N Kasempa (NMZB), Kasusu (NMZB), Kazungula (NMZB), Livingstone (NMZL), 8 km E Lusaka (BM), Mbala (BM), Monze (NMZL), Niamkolo (BM, MCZ), Sakeji (NMZB), Salujinga (AMNH), Sandaula Plain (NMZB), Senanga (TM), Shimbini (NMZB). Kabwe; Lusaka (Schiøtz 1975). MALAŴI. Chelinda Bridge (NMZB, USNM), Chisambo (NMZB), Chitipa (USNM), Kambwe (USNM), Limphasa Dambo (NMZB), Livingstonia (USNM), Lujeri (NMZB), Makoka A.R.S. (BM), Mangoche (BM), Nkhota Kota (NMZB), Rumpi (USNM), Thyolo (TM), Vwaza Marsh (NMZB). Chibotela; Nchisi Mt. (Loveridge 1953*a*), Chisenga; Kaulime; Njakwa (Stewart 1967). MOZAMBIQUE. Beira (NM), Chapala (NMZB), Garuso (NMZB), Gorongoza Mountain (NMZB), Maforga (NMZB), 10 km SSE Vila Gouveia (NMZB). ZIMBABWE. Albany Farm (NMZB), Beatrice (NMZB), Bembezi (NMZB), Bikita (NMZB), Braeside (NMZB), Bulawayo (NMZB), Bundi Valley (NMZB), 5 km N Chivhu (NMZB), Christon Bank (NMZB), Craiglee (NMZB), Dabuka (NMZB), Dowa (NMZB), Gulati C.L. (NMZB), 29 km N Gweru (NMZB), Harare (NMZB), Hartley

(NMZB), Hazelside W (NMZB), Honey River Bridge (NMZB), Inyangombe River (NMZB), Kandarianza Pan (NMZB), Kazungula (NMZB), KweKwe (NMZB), Lake McIlwaine N.P. (NMZB), London Farm (NMZB), Lusulu (NMZB), Mabelreign (NMZB), Maleme Dam (NMZB), Mangula (NMZB), Marondera (NMZB), Masvingo (NMZB), Merrywaters (NMZB), Mount Hampden (NMZB), Mount Selinda (NMZB), Mutare (NM, NMZB), Mutoko (NM), Mvuma (NM), Mvurwe (NMZB), Ngorima Reserve (NMZB), Nyahodi River (NMZB), Nyamaziwa (TM), Nswafugi Dam (NMZB), Outward Bound School (NMZB), Reenen (NMZB), Rukute Farm (NMZB), Sable Park (NMZB), Selborne (NMZB), Silverstreams (NMZB), Togwe Wilderness Area (NMZB), Udu Dam (NMZB), Umfeseri (NMZB), Vumba (NMZB), Worlds View N & S (NMZB), Zambezi River, Kazungula (NMZB), Zewa (NMZB).

Hyperolius benguellensis (Bocage)

Rappia benguellensis Bocage, 1893:119. Caota, Angola. Syntypes (vide Perret 1976) destroyed in the Museu Bocage, Lisbon.
Rappia granulata Boulenger, 1901:4, pl. 2, fig. 3. Pweto, Lake Mweru, Zaïre. Holotype in the Musée Royal de l'Afrique Centrale, Tervuren.
Rappia oxyrhynchus Boulenger, 1901:5, pl. 2, fig. 4. Pweto and Lofoi, Zaïre. Syntypes in the Musée Royal de l'Afrique Centrale, Tervuren.
Hyperolius granulatus; Broadley 1971:121, Stevens 1974:10, Schiøtz 1975:100, Poynton 1982:70.

Diagnosis. Size of breeding males about 19–21 mm. Canthus straight, snout elongated and pointed, projecting well beyond mouth, somewhat shark-like in side profile, head width/body length 27–31 %. Tibia length usually more than half distance from nostril to urostyle tip, sometimes equal to half. Main part of webbing tending to fall short of middle subarticular tubercle of fourth toe on inner side, sometimes not even reaching it on inner side; joining third toe around distal subarticular tubercle. A pair of light dorsolateral and paravertebral bands present at least in juveniles, formed usually by an absence of melanophores in those areas rather than by white pigmentation. Dark spots not forming a mid-dorsal line (see Remarks). Ground colour of juveniles red-brown (not green as in *nasutus*).

Description. A small-sized species characterised by a pointed snout, shark-like in profile. Markings as in Diagnosis.

Habitat. An open savanna or grassland species. J. P. Loveridge (1976) has discussed the habitat selection and water conservation of *H. nasutus* and this species (apparently figured in his fig. 2).

Remarks. Specimens resembling *H. nasutus* but showing a pair of light paravertebral bands identical with or approaching the syntypes of *Rappia oxyrhynchus* Boulenger (1901, pl. 2, fig. 4) have been found in more upland and western areas of the Zambesiaca area. The markings contrast with the 'typical' *nasutus* markings of a mid-dorsal line of dark dots and no light paravertebral bands (although the holotype itself lacks a mid-dorsal or any other line of dots). Individuals showing the *oxyrhynchus* markings have been collected mainly in upland areas of Zimbabwe, west of the Luangwa Valley in Zambia, scattered localities in Botswana, Namibia and Angola, but they have not appeared in collections from eastern Zambia, Malaŵi, Mozambique and Natal (Poynton 1982), apart from Stevens' (1974) Malaŵi record of Zomba Plateau.

There appears to be no difference in habitat preference shown by individuals with the *oxyrhynchus* and *nasutus* markings, and the call of the *oxyrhynchus* type has not been recorded (Schiøtz 1975). Boulenger separated *oxyrhynchus* from *nasutus* on the latter's more distinct webbing, lack of skin granulations and longer hind limbs. Variation in series tends to blur these distinctions, and Schiøtz (1975:100) reported 'failing to see anything indicating the presence of two species'. As discussed below, it is the case that a single series can present not only both marking patterns on separate individuals, but both patterns on the *same* individual, as well as individuals with quite indeterminate markings. The tendency for the *oxyrhynchus* type of markings to occur mainly in upland localities could turn out to be some environmentally triggered polymorphism rather than the indicator of genetic differentiation of taxonomic significance; but until the situation is clarified, it seems advisable to maintain nomenclatural recognition of the two patterns, and provisionally interpret the indications of an east–west geographical patterning as suggesting two different species that have undergone widespread sympatric hybridisation (Poynton 1982). Clarification of the situation will depend on genetical analysis and more fieldwork.

In a detailed study of material from the Upemba National Park, Laurent (1957) argued that markings are correlated with the degree of webbing, thereby demonstrating the real existence of two species, despite some nonconforming 'hybrids'. Laurent believed that *oxyrhynchus* is a synonym of the short-webbed *granulatus*, described by Boulenger in the same 1901 paper, *oxyrhynchus* simply being the juvenile pattern, which is usually lost in large specimens. Boulenger separated *oxyrhynchus* from *granulatus* on its 'museau pointu', and indeed we can confirm that the type and only specimen of *granulatus* has a relatively blunt snout, but Laurent recorded that variation in the shape of the snout prevented it from being a reliable character—indeed, he recorded that the snout shape can vary in one individual according to the position of the pre-maxillas. The single adult holotype of *granulatus* does not possess *oxyrhynchus* markings, leaving reduced webbing as the only 'character' in common—an unreliable feature, as our evidence to be presented below suggests. We are not convinced that Laurent's synonymising of *oxyrhynchus* and *granulatus* is correct, but in the interests of nomenclatural stability, we adopt the practice started by Laurent (1957) of referring individuals with *oxyrhynchus* markings to *granulatus*, and we follow Perret (1976 and in litt.) in referring both of these to *benguellensis* Bocage, even though the types of *benguellensis* were destroyed in the Museu Bocage before we had the opportunity to re-evaluate the situation.

There is no doubt that the characters which are currently in use are inadequate to separate all available specimens into '*nasutus*' and '*benguellensis*' categories, as the following discussion will show, and it is easily conceivable that the material listed here as '*benguellensis*', and also '*nasutus*', will be shown by field and other studies to be composite. As already mentioned, the situation seems to be further complicated by hybridisation. The *nasutus–benguellensis* complex is taxonomically the most poorly resolved of all the Zambesiaca *Hyperolius*, and it appears to offer particular scope for studies in evolutionary dynamics during the Quaternary.

Laurent (1957) presented three lines of evidence to uphold specific distinction between *nasutus* and *benguellensis (granulatus)*.

(1) A correlation between the development of webbing and the juvenile markings (ie the *oxyrhynchus* pattern is correlated with reduced webbing).

(2) A correlation between the development of webbing and degree of pigmentation in adults (in *nasutus*, less than $1\frac{1}{3}$ phalanges of the third toe free correlated with less than five melanophores on arm; in *benguellensis*, more).

(3) A bimodal variation in the degree of webbing between the third and fourth toes in a random sample from Mukana which includes both types.

Material which appears to offer analysis along Laurent's third line of evidence comes from Silverstreams, near Chimanimani, Zimbabwe (NMZB 7513). Thirty-nine adult males show a range of markings from clear paravertebral banding (*oxyrhynchus* pattern) to no light dorsal bands but with a midline of melanophores (typical *nasutus* pattern), the latter being slightly in the minority. Using Laurent's measurements on this material ('la distance minimum entre le bord de la palmure étendue entre les 3e et 4e orteils et le point d'intersection des axes des 1er et 2e métatarsiens, et la longueur libre de palmure du 4e orteil du côté interne'), no bimodal variation was shown. When ten frogs were taken at either end of the range of variation in markings, the means for the degree of webbing were: *oxyrhynchus* pattern 1,64 ($\sigma = 0{,}13$), *nasutus* pattern 1,63 ($\sigma = 0{,}23$). These means would place both samples in Laurent's range for his *granulatus (benguellensis)* material, but comparison of absolute values is hazardous because the Silverstreams series is fairly desiccated and probably yields a lower set of readings than would a fresh series. Nevertheless, this series does not clearly support Laurent's third line of evidence favouring the separation of *nasutus* from his *granulatus (benguellensis)* on the basis of webbing.

However, it may be noticed that the range of variation in the *nasutus* patterned Silverstreams specimens ($\sigma = 0{,}23$) is much greater that the specimens with the *oxyrhynchus* pattern ($\sigma = 0{,}13$). One typical *nasutus* specimen has webbing reaching almost to the disc of the third toe, a degree of development which is occasionally found in other material of the *nasutus* pattern, but not of the *oxyrhynchus* pattern. The range of variation in webbing in *nasutus*-type specimens from other parts of south-east Africa in fact appears to coincide with the Silverstreams series, the web joining the third toe anywhere between the disc and the distal subarticular tubercle. Specimens in the Silversteams series with *oxyrhynchus* patterning fall within the range of variation of the *nasutus*-type specimens, but occupy only the lower part of the range. The coincidence of the two means might, in consequence, seem surprising, but can be accounted for because the variation in *nasutus* material is skewed, the majority having relatively short webbing. This situation appears to hold generally for the eastern part of the range, but limited material from Botswana and Zambia gives some indication that extensive webbing is more common in *nasutus* as one goes west; consequently differences in the means of *nasutus* and *benguellensis* material could be expected. In a Transvaal Museum series of eleven specimens from Piajo, Chief's Island (1922 B2), however, there is no correlation between the degree of webbing and the range of markings, which is 3 *nasutus*, 4 indeterminate, 1 *nasutus* + *oxyrhynchus* (prominent mid-dorsal line of dark spots + light paravertebral lines), and 3 *oxyrhynchus*.

South-east African material also does not support Laurent's first two lines of evidence for the separation of *nasutus* and *benguellensis*. A lack of clear differences between the degree of webbing and the juvenile markings has already been noted. Laurent himself noted that his second line of evidence, involving degree of webbing and of pigmentation, does not hold for all his Upemba material, and no marked correlation between degree of webbing and pigmentation is shown in the Silversteams series or any other large series examined from south-east Africa.

Evidently a finer method of analysis is needed to resolve the taxonomic and geographic picture. As state earlier, genetic and more extensive field studies are wanted: the evolutionary interest of this possible case of complex east–west and upland–lowland differentiation (Poynton 1982) seems worth the effort.

Distribution. See Poynton 1982, fig. 5. Zomba Plateau of Malaŵi, mainly in upland areas of Zimbabwe, west of Luangwa Valley in Zambia, scattered localities in Botswana, Namibia, Angola, Zaïre.

Localities. BOTSWANA. Piajo (TM). ZAMBIA. Monze (NMZL), Ngoma (NMZB). 16 km N Kafue Bridge; Mazabuka (Schiøtz 1975). MALAŴI. Zomba Plateau (Stevens 1974). ZIMBABWE. Atlantica E.R.S. (AJL), Braeside (NMZB), Gokwe (TM), Gulati C.L. (NMZB), 20 km N Gweru (NMZB), Harare (BM, TM), Lusulu (NMZB), Maleme Dam (NMZB), Mangula (NMZB), Mare Dam (NMZB), Merrywaters (NMZB), Mutoko (NM), Prince Edward Dam (AJL), Retreat Farm (NMZB), Schiota Pans (NMZB), Sebakwe Bridge (NMZB), Silverstreams (NMZB), Sote Source (NMZB), Warren Hills (NMZB).

Hyperolius parkeri Loveridge

Hyperolius parkeri Loveridge, 1933:410. Mogogoni Swamp, south of Dar es Salaam, Tanzania. Holotype in the Museum of Comparative Zoology at Harvard.

Hyperolius parkeri rovumae Loveridge, 1942:410. Kitaya, Rovuma River, Tanzania. Holotype in the Museum of Comparative Zoology at Harvard.

Diagnosis. Size of breeding males about 20–24 mm (females in this species are smaller, Schiøtz 1975). Canthus straight, snouth elongated and pointed, projecting beyond mouth, head width/body length 29–33 %. Tibia length more than half distance from nostril to urostyle tip. Main part of webbing passing middle subarticular tubercle of fourth toe on both sides, reaching just beyond distal tubercle on outer side, reaching it on inner side and continuing as a fringe. Breeding males with dark ventral asperities (see Description).

Description. A fairly small-sized species with pointed snout, not unlike *H. nasutus* in general proportions, but snout not projecting so strongly, and webbing more extensive. Green, yellow to brownish in life, with a light canthal and dorsolateral band usually visible, always with a dark brown border (which may be interrupted) above and below. A few scattered dark spots on the back. The markings could be confused with *H. mitchelli*. Breeding males with dark asperities on undersurface of feet, sometimes also the whole leg and posterior part of ventrum. Vocal gland not prominent, with only a relatively small transverse fold posteriorly.

Habitat. Collected on reeds by a small, sluggish stream in evergreen forest—

savanna mosaic near Dondo, associated with *H. tuberilinguis* and *H. argus*. A female laid 36 eggs on the underside of a reed about 30 cm above water-level.

Distribution. Eastern coastal lowlands from Mozambique to Kenya.

Localities. MOZAMBIQUE. Dondo (NMZB).

Hyperolius bocagei Steindachner

Hyperolius bocagei Steindachner, 1867:51, 'Angola'. Holotype in the Naturhistorisches Museum, Vienna. Broadley 1971:121.

Diagnosis. Size of breeding males about 23–26 mm. Canthus curved, snout truncated, sometimes obtusely pointed, head width/body length 34–36 %. Tibia length more than half distance from nostril to urostyle tip, but sometimes only just. Main part of webbing level with middle subarticular tubercle of fourth toe, reaching distal tubercle on outer side and continuing as a well-developed fringe.

Description. Juveniles with a dark line along canthus, continuing behind upper eyelid to sacral area; scattered dark dots over back and upper surface of limbs. In adults dorsolateral line tends to break down into isolated strips or spots, and in females may even become lost. The dorsal spotting and canthal line tends to remain, but specimens of both sexes may be particularly featureless. In life the background colour is a somewhat variegated yellow to green to dark brown. Males in breeding condition have a heavily pigmented backward extension of the gular gland, somewhat more conspicuous than in *H. marmoratus* males, but in general morphology *bocagei* is very similar to *marmoratus*. The webbing is somewhat more deeply incised in *bocagei*, the main part being level with the middle subarticular tubercle of the fourth toe on both sides, whereas in the *marmoratus* subspecies the main part of the webbing passes this tubercle at least on the outer side.

Similarities between *bocagei* and *kachalolae* are noted under that form.

Habitat. No data available.

Remarks. The material listed here has not been compared directly with the type, but it is certainly conspecific with specimens from Angola and Zaïre identified as *bocagei* by Laurent. The female illustrated by Steindachner has no markings apart from the 'schwarzlichen Punkten', a featureless condition that can be shown by both sexes, although appearently more usually in females (Laurent 1954).

Distribution. Angola, southern Zaïre, western Zambia.

Localities. ZAMBIA. Isoka (BM), Isombu (NMZB), Lucheche (BM), Mungwi (BM).

Hyperolius marmoratus Group

The procedure adopted in this study for treating the various species or subspecies of amphibians seems inappropriate for the marmorate reedfrogs, where so many systematic and nomenclatural uncertainties still exist. The southern African forms treated in the literature of the last decade as subspecies variously of *marmoratus, viridiflavus, marginatus* and *parallelus* all conform to a basic morphological pattern, which is outlined here as a diagnosis to differentiate the group of marmorate frogs from other forms of *Hyperolius*. The currently recognised subspecies will then be treated individually, after a general review.

Diagnosis. Size of breeding males about 27–43 mm. Canthus curved, snout truncated, head width/body length 32–38 %. Tibia length more than half distance from nostril to urostyle tip, but often only slightly more. Main part of webbing passing middle subarticular tubercle of fourth toe on outer side, but usually only level with it on the inner side, reaching distal tubercle on both sides and continuing as a narrow fringe.

Habitat. Typically found calling in abundance in reedbeds of ponds, swamps or sluggish rivers, but males also call on waterside grasses, bushes or trees, or in floating vegetation. Eggs laid in water.

Remarks. Reasons for treating members of the *marmoratus* group in southern Africa as subspecies of *marmoratus* Rapp have been discussed by Laurent (1983) and Poynton (1985*a*). We follow Laurent (1976*b*) in placing *nyassae* in this group, rather than in *viridiflavus* as conceived by Schiøtz (1975), although this could be questioned. De Fonesca & Jorque (1979) have reported this form together with *marginatus* at Manjanene Dambo, about 25 km south-west of Nkhata Bay, Lake Malaŵi. There were reported to be 'enormous numbers' of *marginatus*, but 'only a few specimens' of *nyassae*. No material was collected, but it might be relevant that the NMZB Nkhata Bay series of *marginatus* is unlike other Malaŵi material in having a marginless dorsal patch. Bearing in mind the complexities shown in the zone of contact between forms of *marmoratus*, discussed by Poynton (1985*a*), it would seem premature to reject subspecific status for *nyassae* and *marginatus* until more material becomes available. De Fonesca (in litt.) himself advocated caution.

The delimitation of nearly all currently recognised subspecies of *marmoratus* is, it must be admitted, still largely a matter that remains open to question. At present the different taxa are characterised by dorsal colour pattern, as recognised in mainly small samples from scattered localities, without the biological significance of this patterning being at all clear, and without taking into account other features such as lateral subdermal darkening[1] which, if used as taxonomic characters, could produce conflicting classifications. Some of these characters are considered by Schiøtz (1971). The existing delimitations and definitions of subspecies are probably more liable to revision in the western half of the Zambesiaca area than elsewhere, since topography and climate evidently determine more clear-cut ranges in the east, where ranges tend to conform to general zoogeographical patterns. In the more featureless plateau areas to the west, however, the degree of variation and merging may eventaully prove to defeat normal nomenclatural procedures.

Locality records of the *marmoratus* material examined in this study are plotted according to the currently recognised subspecies in Fig. 2.

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[1] This 'subdermal darkening' is developed to a varying degree of intensity in females, and less often and intensely in males, in *marmoratus* of Zambia and western Zimbabwe. The darkening is the result of melanocytes and pigment on both outer and inner surfaces of the muscular body wall. Its histology and function deserves study.

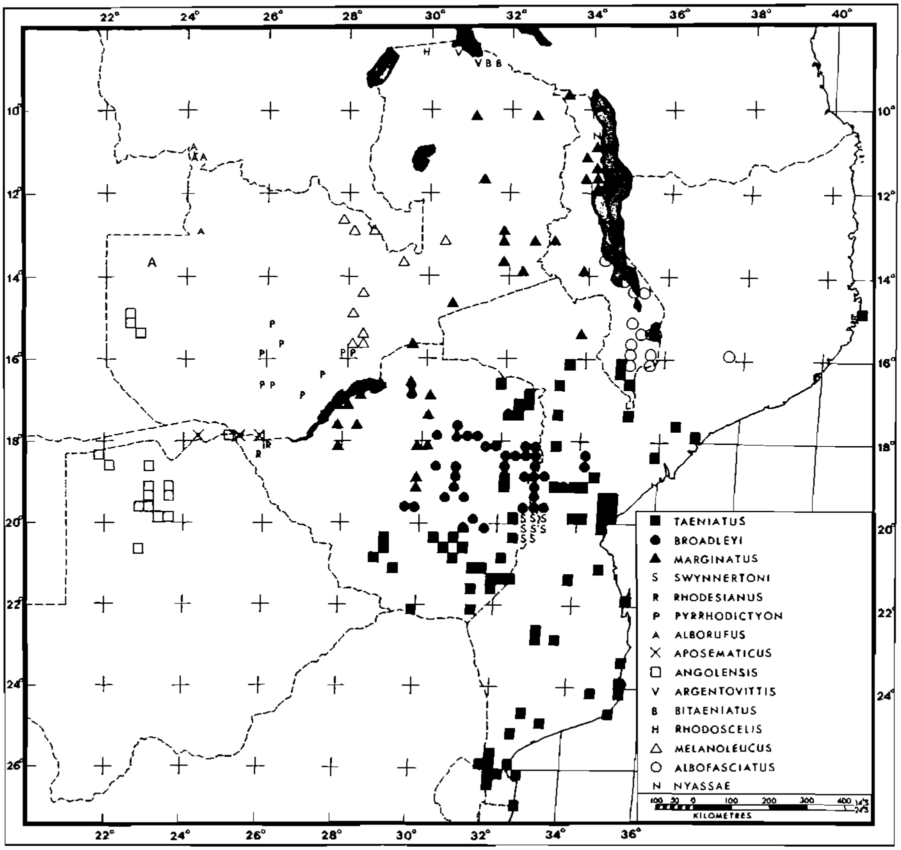

Fig. 2. Distribution of the subspecies of *Hyperolius marmoratus* in the Zambesiaca area.

Hyperolius marmoratus taeniatus Peters

Euchnemis viridiflavus (not Duméril & Bibron); Bianconi 1850.
Hyperolius taeniatus Peters, 1854:628. Boror, Mozambique. Holotype in the Zoologisches Museum, Berlin. Peters 1882:166.
?*Hyperolius citrinus* Günther, 1864:311. Zambezi. Peters 1882:163. Holotype in the British Museum, London.
Hyperolius granulosus Peters, 1866:891. Capanga, east of Tete. Syntypes in the Zoologisches Museum, Berlin. Peters 1882:161.
Hyperolius variegatus Peters, 1882:8. Cabaceira: Quelimane; Boror. Syntypes in the Zoologisches Museum, Berlin. Peters 1882:167.
Rappia marmorata (not Rapp); Pfeffer 1893:27.
Hyperolius marmoratus (not Rapp); Parker 1930:902. Cott 1932:479.
Hyperolius bayoni (not Boulenger); Parker 1930:902, Cott 1932:479.
?*Hyperolius dermatus* Ahl, 1931:382. Type lost. Cabayra, Mozambique.
Hyperolius cinctiventris (not Cope) (part); Hoffman 1944:178.
Hyperolius horstockii horstockii (not Schlegel); Hoffman 1944:179.
Hyperolius marmoratus marmoratus (not Rapp); Loveridge 1953*b*:145.
Hyperolius marmoratus taeniatus Peters, Laurent 1951*a*:34 & 1951*b*:385 & 1961:83 & 1965:2 & 1976*b*:101, Poynton 1964*a*:197 & 1964*b*:219 & 1966:31 & 1985*a*:179, Stewart 1967:148.
TAE Schiøtz 1971:63.
Hyperolius viridiflavus taeniatus Peters, Stevens 1974:11, Schiøtz 1975:214.

Description. Characteristic pattern composed of five light bands; a middle one running from tip of snout to vent, a paravertebral pair running from upper surface of eyelids to base of leg, and a lateral pair from lower half of eye, becoming continuous with ventrolateral light area posteriorly. Light bands separated by four black bands; a paravertebral pair running from canthus rostralis to either side of urostyle tip, and a dorsolateral pair (also starting from canthus) passing along outer edge of eyelid, and continuing backwards from upper half of eye to near base of leg. A less regular lateral black line, running from lower margin of eye over arm and continuing posteriorly, demarcates the lateral pair of light bands. The five light and four black bands are parallel and subequal in width. The light bands may have a thin red or orange line running down the middle; this tends to fade in alcohol. No lateral subdermal darkening.

The most usual variations, all kinds of which may occur in a single series, are as follows: middle light band may have a lateral branch to eyelid on one or both sides, forming an interocular bar; paravertebral light bands (and more rarely the middle band) may become interrupted to form a series of isolated bands or dots, or less commonly a black band becomes interrupted by a transverse linking of two white bands. Black lateral line may be very broken, irregular or absent, so that only three light band are evident.

Tibial markings typically one or two straight longitudinal dark lines, which in a single series may become wavy or broken and/or joined by cross-lines leading to cross-banding and marbling. Irregularities in tibial markings need not be associated with irregularities in dorsal pattern: for example, there can be a very regularly striped dorsum with marbled tibia. Gular area unmarked to heavily marbled or vermiculated with white and black; red present in white areas.

Characteristic juvenile pattern: sacral patches projecting strongly almost to arm insertion as a tapering dark brown band, and a mid-dorsal dark band. A pair of broad lateral dark brown bands, well demarcated by a light line of the dorsal border. The dorsal bands may be lacking, with only the dorsal border of the lateral bands showing, rarely no bands discernible (specimens killed in bright light), although dark brown dots may be present (Peters's *granulosus*). One NMZB specimen from 15 km SE Vila Franca do Save, collected with a typically striped adult, has rounded sacral patches and a dark interocular patch, which is the 'hourglass' pattern (Schiøtz 1971, fig. 3) found in most *marmoratus* subspecies, differing from Schiøtz's figure only in that the occipital patch has a fine backward extension over the scapular region. It is not clear whether this specimen can be included in the variation of *taeniatus*. The locality (2134 B1) is in the central part of the known range of this form. The juvenile pattern will be considered further under Remarks.

Remarks. Evident intergrades between *taeniatus* and *marmoratus* typify collections made in the Lake St Lucia–Richards Bay area of Natal. Intergrades between *taeniatus* and *broadleyi* are discussed by Poynton 1985*a*. Collections have not yet been made in the zone where *taeniatus–swynnertoni* intergrades might be expected.

The striped juvenile pattern of *taeniatus* has been considered by Laurent and by Schiøtz to differ from the 'hourglass' pattern of other *marmoratus* subspecies and to be more like the *viridiflavus* pattern (Schiøtz 1971, p. 25, fig. 3). But the pattern in *taeniatus* results from a forward projection of the sacral patches, which is shown in several *marmoratus* subspecies even if taken to an extreme in *taeniatus*, and a backward projection of the occipital patch, also shown in various configurations in other subspecies. The *taeniatus* pattern is not the same as the 'striped pattern' of *viridiflavus* figured by Schiøtz (1971, fig. 3) and we see no reason to place *taeniatus* outside the acceptable range of variation of the *marmoratus* hourglass pattern. The occurrence of a specimen with a fairly typical hourglass pattern well within the range of *taeniatus*, noted above, does not therefore seem to us to be particularly anomalous.

Distribution. The Mozambique Plain south to Lake St Lucia, Natal, and adjoining areas of Swaziland, Transvaal, Zimbabwe and Malaŵi.

Localities. See Fig. 2. MALAŴI, Chikwawa (TM), Chipata (NMB), Chiromo (NMB), Sucoma Estate (AJL), Nsanje (Loveridge 1953*b*). MOZAMBIQUE. Amatongas (NM, NMZB), Banhinhe Swamps (TM), Beira (BM, NMZB), 16 km NE Beira (NMZB), Boane (TM), Chambajojo (NMZB), Charre (BM), Chigubo (TM), 40 km WNW Chigubo (TM), Chimonzo (TM), Dondo Forest (TM), 8 km NE Dondo (NMZB), Estatuane (NMZB), Fambani (BM), Goinha Plain (TM), Gorongosa Game Reserve (TM), Grudja (NMZB), Guija (TM), Guro (NMZB), Inchope (NMZB), Inhaca Island (NM, NMZB, TM), Inhambane (ZMB), 8 km E Jangamo (TM), Lower Pungwe Bridge (NM), Lower Revue Bridge (NMZB), Maforga (NMZB), Magude (TM), Manga (NMZB), Maputo (BM, NM, TM), Massinga (NMZB), Mdimba (TM), Morromeu (TM), Mt. Meponduine (NMZB), Muda/Lamego (NMZB), Namaacha (NMZB), Nova Lusitania (TM), Nova Sofala (NMZB), Panda (NMZB), Ponte do Calichane (NM), Ponta do Ouro (TM), Ponte do Pungwe (NMZB), 10 km SSE Ressano Garcia (NMZB), Tete (NM), 15 km SE Vila Franca do Save (NMZB), 30 km ESE Vila Gouveia (NMZB), Vilanculos (TM), Viola (NMZB), Xiluvo (NMZB), Zavora (NMZB), Zinave (NMZB), Boror; Cabaceira; Capanga; Quelimane; Chire River; Tete (Peters 1882), Vila Pery (Laurent 1951*a*), Shise (Laurent 1961). ZIMBABWE. Beitbridge (NMZB), Birchenough Bridge (NMZB), Blanket Dam (NMZB), Chibi (NMZB), Chikore (NMZB), Chipinda Pools (NMZB), Chiredzi (NMZB), Chisumbanje (NMZB), Fishan (NMZB), Gonakudzingwa Koppies (NMZB), Irisvale (NMZB), Kyle National Park (NMZB), Longueville Ranch (NMZB), Lower Nuanetsi River (NMZB), Lundi River Bridge (NM), Machinawa Pan (NMZB), Malugwe Pan (NMZB), Marhumbini (NMZB), Mbalabala (NMZB), Mubagwashe (NMZB), Mutoko (NM), 16 & 40 & 56 km NE Mutoko (NMZB), Nyadekese Dam (NMZB), Nyaruwe Hill & 9,5 km S (AJL), Razi Dam (NMZB), Sabi Drift (NMZB), Sabi/Lundi Confluence (NMZB), Sungwisi Weir (NMZB), Triangle (NMZB), Tshabezi River Bridge (NMZB), Tsuro (NMZB), 20 km SE West Nicholson (NMZB), Zimbabwe Ruins (NMZB).

Hyperolius marmoratus broadleyi Poynton

Rappia marmorata (not Rapp); Hewitt & Power 1913:170.
Hyperolius marmoratus (not Rapp); FitzSimons 1958:211.
Hyperolius marmoratus broadleyi Poynton, 1963:328. Mutare, Zimbabwe. Holotype in the Natural History Museum of Zimbabwe, Bulawayo. Poynton 1964*a*:198 & 1985*a*:179.
BRO Schiøtz 1971:40.
Hyperolius marginatus broadleyi; Laurent 1976*b*:97.

Description. Characteristic pattern: a light mid-dorsal band running from tip of snout to vent, and a pair of dorsolateral light bands running from edge of upper eyelid and upper half of eye to base of leg, bordered laterally by a dark band commencing at the lower half of the eye. Dorsal and lateral light bands separated by a broad dark band running from canthus rostralis over upper eyelid almost to vent, the light mid-dorsal band being only half the width of the black band to either side (width dorsal light band/width paravertebral black band averages 47 % in 20 paratypes). Light bands usually with a red line in the centre. No lateral subdermal darkening.

The most usual variations (excluding marginal populations, discussed by Poynton 1985*a*), all of which may occur in a single large series, are: dorsolateral light bands may curve obliquely outwards and continue into light ventral area at position of elbow of folded arm, or the band may lose its lower margin because the lateral dark band breaks up into spots or disappears entirely. The light bands may become broken into discontinuous lines. The lateral edges of the dark bands may become saw-toothed or more extensively invaded by light vermiculations in the sacral region, and, rarely, more anteriorly. Occasionally, one or a few light spots occur in the dark bands.

Tibial markings vary from a single, irregular dark longitudinal band to a line of dark patches or spots, to light and dark vermiculations. Gular region usually unmarked, sometimes with black speckling or marbling, with or without red in the white areas.

Juvenile pattern: usually unmarked dorsally; a light dorsolateral streak or line may run backwards from the upper eyelid. Sacral patches not normally present, at best indistinct; rounded in shape.

The complex situation where the ranges of *broadleyi* and *taeniatus*, and *broadleyi* and *swynnertoni*, come into contact has been discussed by Poynton 1985*a*. A limited tendency to form a mottled or vermiculated pattern reminiscent of *swynnertoni* is shown in eastern highland material to the north of the Chimanimani area. Occasional specimens show an invasion of the dark bands by light spots and vermiculations in series from Gairezi Bridge and Mare Dam, Nyanga District, and also Imbeza and Engwa in the Mutare District. Broadening of the light bands and corresponding narrowing of the dark bands is shown at Engwa and Odzani, Mutare District. It is unclear whether these trends are genetically related to the appearance of *swynnertoni* further south. The presence of *taeniatus* in the adjoining lowlands could also be a factor.

To the north-west, *broadleyi* intergrades with *marginatus*. A range from one to the other form was illustrated by Schiøtz (1971, fig. 73) in a series from Karoi. Similar series could be looked for to the west of Harare, judging from a specimen (NMZB 766) collected at the Harare Snake Park in 1960 which has the uniformly coloured back of *marginatus*, but lateral marbling more like *broadleyi*, and marbled tibiae. Two typical *broadleyi* have subsequently been collected there.

The dorsal patterns of 'typical' *broadleyi* and *melanoleucus* are virtually identical. Some differences between the two forms are noted under *melanoleucus*.

Distribution. The eastern Zimbabwean highveld and its fringes and outliers in Mozambique.

Localities. See Fig. 2. MOZAMBIQUE. Chemezi (NMZB), Garuso (NMZB), Gorongoza Mountain (NMZB), Maforga (NMZB), Mavita (NMZB), Vila de

Manica (NMZB), Vila Paiva de Andrada (NMZB). ZIMBABWE. Arcturus (NMZB), Atlantica Research Station (AJL), Banti (NMZB), Bikita (NMZB), Biriviri River (NMZB), Bomponi (NMZB), Cashel (NMZB), Chisawasha (SAM), Chivhu (NMZB), 5 km N Chivhu (NMZB), Driefontein Mission (AM, NMZB), Dunblane (NMZB), Ellesmere Farm (AJL), Engwa (NMZB), Featherstone (NMZB), Foliot Farm, Karoi (NMZB: *marginatus* × *broadleyi* intergrade), Gairezi Bridge (NMZB), Glen Cova (NMZB), Good Hope Farm (NMZB), Gwebe Bridge (NMZB), Harare (AM, NMZB), Haroni River (NMZB), Haroni/Rusitu Confluence (NMZB), Henry Hallam Dam (AJL), Imbeza (NMZB), Inyanga Village (NZMB), Karoi (NMZB), Koppies Farm (AJL), Kutama Mission (AJL), Lake McIlwaine (AJL, NMZB) Makurupini Valley (NMZB), Malugwe Pan (NMZB), Mare Dam (AJL, NMZB), Marondera (NMZB), Matinedza (NMZB), Mazoe (BM), Melfort (NMZB), Mount Dombo (NMZB), Mount Hampden (NMZB), Msari River (NMZB), Mutambara (NMZB), Mutare (BM, NM, NMZB), Mutare River Bridge (NMZB), Mutoko (NM), Ngezi Bridge (NMZB), Nyahodi Bridge (NMZB), Nyamakari (NMZB), Nyamazi (NMZB), Nyamaziwa (TM), Odzani Dam (NMZB), Penhalonga (NMZB), Prince Edward Dam (AJL), Rhodes Inyanga National Park (NMZB), Rusape (NMZB), Ruwa (AJL), Saffron Walden (AJL), Shepherds Hotel (NMZB), Shurugwe (NMZB), Somabhula (NMZB), Sote Source (NMZB), Stapleford (NMZB), Sungwisi River Bridge (NMZB), Tandaai (NMZB), The Corner (NMZB), Umfeseri (NMZB), Upper Pungwe River (TM), Vumba (NMZB).

Hyperolius marmoratus marginatus Peters

Hyperolius marginatus Peters, 1854:627. Macanga, Mozambique. Holotype in the Zoologisches Museum, Berlin. Peters 1882:165, Schiøtz 1975:216.
Hyperolius lestagei Laurent, 1943:109. Laupula (near Lake Bangweulu), ?Zaïre. Holotype in the Musée du Congo Belge, Tervuren.
Hyperolius marmoratus lestagei Laurent, 1951*b*:386.
Hyperolius marmoratus marginatus; Poynton 1964*a*:199 & 1964*b*:219 & 1966:32 & 1985*a*:179, Stewart 1967:150, Broadley 1971:124, de Fonesca & Jocque 1979:805.
MAG Schiøtz 1971:67.
Hyperolius marginatus marginatus; Laurent 1976*b*:97.

Description. Characteristic pattern (figured by Peters 1882, pl. 22, fig. 8) a uniform brown back with a darker dorsolateral margin, below which the sides are light apart from red speckling. The dark margin may be absent or may become a thick band, and dark spots may be present in the dorsal area. No lateral subdermal darkening. Juvenile pattern a very well-marked hourglass pattern with somewhat elongated sacral patches. The pattern is often accentuated by a light outline.

Remarks. The unusually well-marked juvenile pattern of this form may be associated with the unusual uniformity of the adult dorsal coloration. This could be a starting point for a study of the significance of the two colour phases. In a single NMZL adult male from Isoka, the dark spots tend to have light centres, giving an overall effect reminiscent of *verrucosus*. A juvenile from the same locality shows the typical *marginatus* juvenile pattern, and without more material available, it seems best for the moment to stretch the acceptable variation of *marginatus* to include the Isoka male.

The only demonstrated intergrading between this form and another is among

NMZB series of *marginatus–broadleyi* from Karoi and west of Harare in Zimbabwe (see under *broadleyi*). It is likely that *marginatus* will be found to merge with *rhodoscelis* between Lakes Bangweulu and Mweru in northern Zambia, judging from similarities in both juvenile and adult patterns (see under *rhodoscelis*).

Distribution. Eastern half of Zambia (from Lake Bangweulu and Lake Kariba) apart from the extreme north-east, northern Zimbabwe, at least western Malawi and south-eastern Tanzania. Due to inadequate collecting east of Lake Malaŵi, it cannot definitely be said that the Tanzanian populations are fully isolated from populations west of Lake Malaŵi.

Localities. See Fig. 2. ZAMBIA. Chipangali (NMZB), Isoka (NMZL), Msoro (NMZB), Mufuwe (NMZB), Nsefu Game Camp (NMZB), Sayiri Court (NMZB), Kachalola; Kasama; 16 km N Mpika; Siavonga (Schiøtz 1975). MALAŴI. Chitipa (NMZB), Lifupa (NMZB), Lilongwe (NMZB), Limphasa Dambo (NMZB), Mzimba (NMZB), Mzuzu (USNM), Nchenachena (NMZB), Njakwa (USNM), Nkhata Bay (NMZB, USNM), Nkwadzi Hill Forest (NMZB), Rumpi (NMZB, USNM); Manjenene Dambo (de Fonesca & Jorque 1979). MOZAMBIQUE. Macanga (Peters 1854). ZIMBABWE. 16 km SSW Chakari (AJL), Chirisa S.A. (NMZB), Gachegache Confluence (NMZB), Harare Snake Park (NMZB), Hunter's Road (NMZB), Karoi (NMZB), Lusulu (NMZB), Mangula (NMZB), Maronga River (NMZB), Mcheri River Gorge (NMZB), Mwenda Estuary (NMZB), Nyanyana Mouth (AJL), Rukute Farm (NMZB, TM), Sapi–Zambezi Confluence (NMZB), Sengwa Confluence (NMZB), Sherwood Block (NMZB), Sinoia Caves (NMZB), Tashinga Camp (NMZB), Umfuli River Bridge (NMZB).

Hyperolius marmoratus swynnertoni FitzSimons

Hyperolius marmoratus (part) FitzSimons, 1939:43.
Hyperolius swynnertoni FitzSimons, 1941:280. Chirinda Forest, Zimbabwe, Holotype in the Transvaal Museum, Pretoria. Poynton 1964*a*:200 & 1985*a*:180.
Hyperolius marmoratus swynnertoni; Laurent 1951*b*:384.
SWY Schiøtz 1971:41.
Hyperolius marginatus swynnertoni; Laurent 1976*b*:97.

Description. Dorsal markings very variable and asymmetrical, ranging from a scattering of dark dots to larger spots to a marbling or reticulation, coarse or fine; or light speckling. No lateral subdermal darkening. Brown males without sacral patch, usually with a light lateral line extending behind each eye.

Remarks. Intergrading of this form with *broadleyi* is described in the section on *broadleyi* and in Poynton 1985*a*. The contact zone with *taeniatus* is at present unexplored.

Distribution. Southern portion of the eastern Zimbabwe uplands and adjoining Mozambique.

Localities. See Fig. 2. MOZAMBIQUE. Espungabera (NMZB), Mucrera River (NMZB). ZIMBABWE. Albany Farm (NMZB), Bundi Valley, (NM, NMZB), Chipinga (NMZB), Chirinda Forest (BM, TM), Dunblane (NMZB), Haroni River, Chimanimani (NMZB), Haroni/Rusitu Confluence (NMZB), Makurupini

Valley (NMZB), Merrywaters (NMZB), Musapi River (NMZB), Ngorima C.L. (NMZB), Nyahodi River (NMZB), Silverstreams (NMZB), Umzilizwe River (BM, NM, NMZB).

Hyperolius marmoratus rhodesianus Laurent

Hyperolius marmoratus rhodesianus Laurent, 1947*b*:294. Matetsi, Zimbabwe. Holotype in the British Museum, London.
Hyperolius rhodesianus; Poynton 1964*a*:201.
RHE. Schiøtz 1971:40.
Hyperolius marginatus rhodesianus; Laurent 1976*b*:96.

Description. Characteristic pattern in life a yellow ground colour with green spots containing grey centres. The colours fade on preservation, leaving lightly to heavily darkened dots as the only clearly discernible pattern. A red marbling or vermiculation present on the belly, which disappears after preservation. Females with lateral subdermal darkening. Juvenile pattern unknown.

Distribution. Extreme north-western portion of Zimbabwe.

Localities. Fig. 2. ZIMBABWE. ?Hwange National Park (NMZB), Matetsi (BM), Matetsi River Bridge (NMZB); Matetsi (Laurent 1947*b*; Schiøtz 1975).

Hyperolius marmoratus pyrrhodictyon Laurent

Hyperolius marmoratus pyrrhodictyon Laurent, 1965:5. Mazabuka, Zambia. Holotype in the Museum of Comparative Zoology, Harvard. Broadley 1971:122.
PYR Schiøtz, 1971:38.
Hyperolius parallelus pyrrhodictyon; Schiøtz 1975:181.
Hyperolius marginatus pyrrhodictyon; Laurent 1976*b*:96.

Description. Characteristic dorsal pattern in life a yellow to brown to olive ground colour, often with lighter spots in which there may be a black centre. This ground colour tends to fade on preservation, so that the light spots become indistinct and only the black centres remain as a discernible marking. The black marks are usually more or less rounded, rarely vermiculated. These lighter spots with black centres may be sparse on the back and more common on the legs (as in the description of the type). A red network or marbling on the belly is generally distinct even in preserved specimens.

Females with lateral subdermal darkening, very evident in some series (eg Choma) but barely so in others (eg Monze). No distinctive juvenile pattern yet seen.

Remarks. Laurent did not compare *pyrrhodictyon* with his *rhodesianus* when describing it. As Schiøtz (1975) has noted, the two forms are very similar. Variation in the degree of ventral marbling in *pyrrhodictyon* is great, and further collecting may show that the possession of alcohol-proof ventral marbling is not in itself sufficient as a diagnostic character.

Distribution. Kafue River and uplands to the south; not reaching the Zambezi at Livingstone, but rest of southern boundary not yet determined.

Localities. See Fig. 2. ZAMBIA. Choma (NMZL), Chunga (NMZB), Dumba River (NMZB), Kabanga (NMZB), Kavula River (NMZB), Mazabuka (NMZB), Monze (NMZL), Namwala (TM), Ngoma (NMZB), Nkala Stream (NMZB). Kafue River Bridge (Schiøtz 1971).

Hyperolius marmoratus alborufus Laurent

Hyperolius marmoratus alborufus Laurent, 1964:153. Cazombo, Angola. Type not traced. Laurent 1965:1, Broadley 1971:122, Laurent 1983:33.
ALR Schiøtz 1971:34.
Hyperolius parallelus alborufus; Schiøtz 1975:185.
Hyperolius marginatus alborufus; Laurent 1976*b*:91.

Description. Generally a light ground colour, with red or red-brown spots, vermiculations or very irregular paravertebral bands. Typically with dark dots around the vent and on the outer surfaces of the limbs. Females with heavy lateral subdermal darkening, varying in males from being heavy to barely discernible. Juvenile pattern: hourglass, with a tendency for occipital patch to project backwards and sacral patches to project forwards.

Distribution. Northern area of western Zambia, and adjoining areas of Angola and Zaïre.

Localities. See Fig. 2. ZAMBIA. Balovale Boma (NMZB), Balovale District (NMZB), Ikelenge (NMZB), Mayau River (AMNH), Sakeji (NMZB), Salujinga (AMNH), Zambezi Bridge (NMZB).

Hyperolius marmoratus aposematicus Laurent

Hyperolius marmoratus aposematicus Laurent, 1951*a*:35. Lealui, Zambia. Holotype in the Muséum National d'Histoire Naturelle, Paris. Laurent 1951*b*:384, Broadley 1971:122.
Hyperolius aposematicus Laurent, Poynton 1964*a* (part):201.
APO Schiøtz 1971:39.
Hyperolius parallelus aposematicus; Schiøtz 1975:183.
Hyperolius marginatus aposematicus; Laurent 1976*b*:96.

Description. Characteristic pattern in life a light cream to yellow to brown, with dark brown to black spots or vermiculation. In the eastern part of the range the darker markings are sometimes arranged loosely in longitudinal rows or irregular lines; in the west a more definite pair of dark paravertebral bands (approaching the *parallelus* pattern) may be present. Irregular red ventral markings present, but disappearing in preserved specimens. Females with lateral subdermal darkening (sometimes only weakly shown in eastern material). Juvenile pattern a complete to broken hourglass pattern, sacral patches with some forward projection, but not passing beyond position of elbow joint.

Remarks. Relationships between this form and *m. angolensis* are discussed under *angolensis*.

Distribution. The Victoria Falls Zimbabwe record (Poynton 1964*a*) is based on a faded NMZB specimen with a snout so pointed as to raise doubts as to whether it is a member of the *marmoratus* group. Eastern Caprivi, north-western Zimbabwe and south-western Zambia, but not west of the Zambesi.

Localities. See Fig. 2. CAPRIVI. Lake Liambesi (TM), ZAMBIA. Dambwa (NMZB), Livingstone (BM, NMZB, NMZL, TM); Lealui (Laurent 1951*a*). ZIMBABWE. Namakurwe Confluence (NMZB), Zambezi Camp (NMZB).

Hyperolius marmoratus angolensis Steindachner

Hyperolius marmoratus var *angolensis* Steindachner, 1867:50. Angola. Holotype in the Naturhistorisches Museum, Vienna.
Hyperolius angolensis; Poynton 1964*a*:202.
ANG Schiøtz 1971:32.
Hyperolius marmoratus angolensis; Broadley 1971:122, Laurent 1983:21, Poynton 1985*a*:180.
Hyperolius marginatus angolensis; Laurent 1976*b*:91.

Description. Brown to reddish markings contrasting with white or cream. These markings range from a fine peppering to dense vermiculation or reticulation to irregular red-brown paravertebral bands that border a light vertebral band, often with an interorbital crosspiece (see Remarks). Females with lateral subdermal darkening, weakly shown to absent in males. Juvenile pattern in Botswana basically hourglass, with sacral patches projecting forward, sometimes joining extensions from the occipital patch. A TM specimen from Lisikili, Eastern Caprivi, has rounded sacral patches, more like *aposematicus*, but a female caught with it shows the adult *angolensis* pattern.

Remarks. Poynton (1964*a*) referred Botswana material of the marmorate reedfrog to *angolensis* with some uncertainty. Schiøtz (1971) noted that specimens he had examined from Botswana and Angola 'are as different from each other as what is normally regarded as different subspecies', but nevertheless included the Botswana material in *angolensis*. In 1975 he tentatively placed this material in *aposematicus*, in view of variation found in that form, but this proposal does not find support in a TM series of what is typical *aposematicus* from Lake Liambezi in the eastern Caprivi. These seven specimens show small to large black spots scattered over a light ground, making them readily distinguishable from all material included here under *angolensis*. Two forms must therefore be recognised. The larger number of *aposematicus* specimens now available show greater variation than the Lake Liambezi series, and even though some Livingstone specimens are closer in markings to *angolensis* than are the Lake Liambezi specimens, accumulating material tends to uphold rather than blur the overall distinctiveness of *angolensis* and *aposematicus*.

Schiøtz noted that Botswana material differed from Angola material in having a wider range of variation in markings and a more reddish ground colour; also, the dark subdermal bands tend to be less developed or lacking in males. Material from western Zambia shows somewhat less variation than Botswana material, in that the finely peppered extreme is absent in the relatively limited amount of material available. Nevertheless, variation is very great. A CNHM series of twelve specimens from Kalabo shows a range from the vermiculated pattern (F–3 of Schiøtz) which is predominant in north-eastern Angola, to a pattern with a single light mid-dorsal band and two dorsolateral bands, separated by a broad pair of paravertebral darker bands (F–1 of Schiøtz). This latter pattern approaches the *argentovittis* pattern, but in the Kalabo series the broad paravertebral bands contain vestiges of another pair of light bands commencing at each upper eyelid. These vestiges are included in the variation of *argentovittis*, at least in the west of its range: in MRAC Upemba material identified as *argentovittis* by Laurent, the overall range of variation is in fact about as great as in the Kalabo material, but the range lies more in the *argentovittis* end of the *argentovittis–angolensis* 'spectrum', some specimens being quite typically *argentovittis*, and even the finest vermiculation shown is not as fine as in the Kalabo series. It is evident that all the variable material from Upemba to Botswana represents a zone of intermingling or hybridisation between western *angolensis* (basically F–3 pattern) and eastern *argentovittis* (basically F–1 pattern), complicated by a further cline from north to south in that there is increasingly fine vermiculation to the south. As the degree of subdermal darkening in the Upemba males is variable, it is not clear whether a cline, suggested by Schiøtz, exists in this feature as well.

This apparent *angolensis–argentovittis* hybrid zone hardly seems to deserve nomenclatural recognition, even though the inclusion of the Zambian and Botswana material under *angolensis* could also seem undeserved. The situation recalls a possible problem in Natal (Poynton 1985*a*), where what could be seen as a hybrid zone between *taeniatus* and *verrucosus* results in *m. marmoratus*. In Natal, however, no single series gives a complete range from the *taeniatus* to the *verrucosus* pattern: despite a wide range of variation from banded to speckled patterns, a distinctive pattern (figured by Rapp) is stabilised over a wide area. A not dissimilar pattern is quite common in Botswana material, but the population as a whole does not appear to have stabilised to anything like the same extent as in Natal. Nomenclatural recognition therefore does not seem as justified as it does in Natal.

Distribution. Eastern Angola, grading into eastern *argentovittis* in a belt from Upemba through extreme south-western Zambia to Botswana and northern Namibia.

Localities. See Fig. 2. BOTSWANA. Boro/Kiri River (TM), Boro River (TM), Chiefs Island (TM), Four Rivers Camp (NMZB), Gugathebe Bridge (TM), Kasane (NMZB), Kiri River (TM), Khwai River (NMZB), Lake Ngami (BM), Maun (NMZB), Maxwee (NMZB), Piajo (TM), Pom Pom (NMZB), Selinda Spillway (NMZB), Sepopa (TM), Shakawe (NMZB), Shorobe (NMZB), Xaxaba (NMZB), Xugana (NM, TM). CAPRIVI. Lianshulu (TM), Lisikili (TM). ZAMBIA. Kalabo (CNHM, NMZB), Kalenga (NMZB), Sandaula Plain (NMZB).

Hyperolius marmoratus argentovittis Ahl

Hyperolius argentovittis Ahl, 1931:345. Ujiji, Tanzania. Holotype in the Zoologisches Museum, Berlin.
Hyperolius callichromus Ahl, 1931:372. Rusizi River, Zaïre. Holotype in the Zoologisches Museum, Berlin. Loveridge 1933:403.
Hyperolius marmoratus argentovittis; Broadley 1971:122, Laurent 1983:16, Poynton 1985*a*:180.
ARG Schiøtz 1971:35.
Hyperolius parallelus argentovittis; Schiøtz 1975:176.
Hyperolius marginatus argentovittis; Laurent 1976*b*:91.

Description. Characteristic dorsal pattern a light (white to yellow in life) mid-dorsal band running from between eyes to above vent. Rest of dorsum brown to red-brown, bordered by an almost black line. A light lateral band running above upper lip, continuing behind eye as a lateral light area continuous with ventrum: no dark lateral band. Dorsal surface of tibia with a fairly regular brown band surrounded by yellow or white.

Variation in Zambian material consists of breaks and bulges in the mid-dorsal band and projections from the lateral light area into the paravertebral dark bands. Vestiges of a dark lateral band, demarcating a light dorsolateral band from the ventrum as in *angolensis* and *melanoleucus*, may be present. It is shown to at least some degree in five of the ten MCZ Niamkolo specimens, and it becomes more common to the south and west: it is the rule in MRAC Upemba material, which shows mingling with the *angolensis* pattern (see under *m. angolensis*). Sometimes a separate light interorbital bar is formed. The tibial bands become correspondingly irregular.

Both sexes with lateral subdermal darkening, but tending to be fainter in males. Juvenile pattern with rounded sacral patches.

Distribution. Shore of Lake Tanganyika in Zambia, extending north-eastwards to Lake Victoria and westwards over Zaïre, intergrading with *angolensis* in central to western Zaïre.

Localities. See Fig. 2. ZAMBIA. Mbete Bay (BM), Mpulungu (NMZB, PEM), Niamkolo (BM, MCZ, TM).

Hyperolius marmoratus bitaeniatus Ahl

Hyperolius bitaeniatus Ahl, 1931:322. Ukonde Unyika, Tanzania. Holotype in the Zoologisches Museum, Berlin.
RHC-Tanzania Schiøtz 1971:62.
Hyperolius viridiflavus bitaeniatus; Schiøtz 1975:211.

Description. In life, 'Dorsum yellowish brown often with a diffuse yellow dorsolateral line' (Schiøtz 1975), sometimes with scattered black spots on the sides and limbs. The yellow dorsolateral line becomes inconspicuous in preserved specimens. Both sexes with lateral subdermal darkening. Juvenile pattern faintly shown, sacral patches with forward projections.

Distribution. Higher ground of north-eastern Zambia (not the environs of Lake Tanganyika) and adjoining south-western Tanzania.

Localities. See Fig. 2. ZAMBIA. Chianka (NMZB), Fwambo (BM), Lucheche (BM), Mbala, (BM, PEM), Mningi Pans (NMZB).

Hyperolius marmoratus rhodoscelis (Boulenger)

Rappia rhodoscelis Boulenger, 1901:3. Pweto, Zaïre, Syntypes in the Musée Royal de l'Afrique, Tervuren, and British Museum (N.H.) London.
Rappia undulata Boulenger, 1901 (part):4. Material from Pweto, Zaïre.
Hyperolius marmoratus rhodoscelis; Laurent (part) 1951*b*:386 & 1965:1 & 1983:27, Broadley 1971:122.
RHC Schiøtz 1971:62.
Hyperolius viridiflavus rhodoscelis; Schiøtz 1975:212.
Hyperolius marginatus rhodoscelis; Laurent 1976*b*:98.

Description. Uniform light yellow dorsally, light brown in alcohol, occasionally with a few small dark spots on the head (usually the sides), near the vent or on the limbs. A bright yellow dorsolateral band usually present in both sexes from neighbouring Zaïre (actually a subdermal band of white tissue attached to the trunk muscles, sometimes also attached to the skin), but not shown in the single specimen known from Zambia. Intense lateral subdermal darkening. Juvenile pattern: hourglass type, lateral borders with light edging (as described in *undulata*), but occipital and sacral patches (if present) not or only faintly edged: edging not as conspicuous as in *marginatus*. Occipital patch sometimes continuing into a scapular patch, or there may be a separate scapular patch.

Remarks. The single Zambian record is based on a NMZB female from Mweru Wantipa which, as Schiøtz (1975) notes, lacks diagnostic characters. The characteristic dorsolateral light band is only faintly shown to completely missing in a MRAC series from Kilwa, and the Mweru Wantipa specimen could represent a population showing the same variation. The strong possibility of this variation merging into the *marginatus* pattern to the south-east needs to be investigated. Reduction and loss of the dorsolateral band is evidently a trend towards the *bitaeniatus* pattern of the Mbala uplands to the east, but it is less clear how the pattern could merge with the *argentovittis* pattern of the adjoining Lake Tanganyika basin.

Distribution. Lower part of the Luapula River, environs of Lake Mweru and Mweru Swamp (Mweru Wantipa).

Localities. See Fig. 2. ZAMBIA. Mweru Wantipa (NMZB).

Hyperolius marmoratus melanoleucus Laurent

Rappia undulata; Boulenger (part) 1901:4. Material from Lofoi, Zaïre.
Hyperolius melanoleucus Laurent, 1941:157. Lukafu, Zaïre. Syntypes in the Musée Royal de l'Afrique Centrale, Tervuren.
Hyperolius marmoratus nyassae (part, not Ahl); Laurent 1951*b*:385 & 1965:3.
Hyperolius aposematicus (part, not Laurent); Poynton 1964*a*:201.
Hyperolius marmoratus melanoleucus; Laurent 1965:2 & 1983:31, Broadley 1971:122.
MEL Schiøtz 1971:36.
Hyperolius parallelus melanoleucus; Schiøtz 1975:179.
Hyperolius marginatus melanoleucus; Laurent 1976*b*:93.

Description. The 'typical' *melanoleucus* pattern in Zaïre, as shown in the type series, consists of three light bands (usually with a red central line) separated by broad dark paravertebral bands, which are usually invaded in the sacral area by projections from the dorsolateral bands (Laurent 1941, pl. 8, fig. F; Schiøtz 1971, fig. 21). In Zambia this 'typical' pattern is to be found, but there is a marked tendency for irregular, asymmetrical invasion of the dark area by the light bands or separate spots or bands, to the extent that only a coarsely vermiculated or reticulated dark patterning may be present. Belly with red spotting or marbling (tending to disappear in alcohol). Females with lateral subdermal darkening, which is present or absent in males.

Juvenile pattern with rounded sacral patches.

Remarks. Specimens from the type series with regular and symmetrical development of the 'typical' pattern cannot be distinguished from 'typical' *broadleyi* on dorsal pattern alone. However, the red ventral markings in both sexes of *melanoleucus* is distinctive, as is also the red and black speckling of the lateral surface of the limbs, and the gular region of practically all males. There seems to be no very clear way of distinguishing some of the more irregularly marked specimens of *melanoleucus* from *aposematicus*, but the presence of fairly 'typical' *melanoleucus* in the highly variable Lusaka material justifies placing specimens north of the Kafue in *melanoleucus* (Laurent 1965, Schiøtz 1971 & 1975) rather than in *aposematicus* (Poynton 1964*a*).

Distribution. Central Zambia north of the Kafue, and south-eastern Zaïre.

Localities. See Fig. 2. ZAMBIA. Chilanga (NMZB), Chingola (DM), 16 km W

Chisamba (AJL), Kitwe (MM), Lusaka (BM, NMZB), 8 km E Lusaka (BM), Nchanga (BM), Serenje (NMZB ex MCZ). Lusaka; Mkushi District; Mwambeshi River; Chikoli River, Serenje (Laurent 1965). Chilanga; Kabwe; 16 & 19 km N Kafue River Bridge; Lusaka; Ndola (Schiøtz 1975).

Hyperolius marmoratus albofasciatus Hoffman

Rappia marmorata (not Rapp); Günther 1895:526.
Hyperolius albofasciatus Hoffman, 1944:178. Limbe, Malaŵi. Holotype in the Nasionale Museum, Bloemfontein.
Hyperolius cinctiventris (not Cope); Hoffman 1944:178.
Hyperolius horstockii (not Schlegel); Mitchell 1946:32.
Hyperolius symmetricus (not Mocquard); Mitchell 1946:32.
Hyperolius marmoratus albofasciatus; Loveridge 1953*a*:350, Laurent 1965*b* (part):4, Poynton 1964*b*:220 & 1966:32, Stewart 1967:153, Dudley 1978:91.
ALF Schiøtz 1971:42.
Hyperolius parallelus albofasciatus; Stevens 1974:10; Schiøtz 1975:187.
Hyperolius marginatus albofasciatus; Laurent 1976*b*:97.

Description. Characteristic pattern a white or yellow mid-dorsal band, with no central red line; rest of back black. Sides same colour as dorsal band, but with a row of black blotches. Variation includes irregularities of the dorsal band and projections from the light lateral area over the back. No lateral subdermal darkening. Juvenile pattern of the hourglass type, but sacral patches tending to 'unite medially and continue forward to the scapular region as a vertebral stripe' (Stewart 1967).

Remarks. The development of a mid-dorsal band in the juvenile pattern, reported by Stewart (1967), recalls the condition in *taeniatus*. Intergrades should be searched for at altitudes between about 200 and 500 m in southern Malaŵi.

Distribution. Uplands of southern Malaŵi and adjoining Mozambique to the east.

Localities. See Fig. 2. MALAŴI. Blantyre (BM, NMZB), Chitala (NMB), Lake Chilwa (NMB), Limbe (NMB), Likabula Rest House (USNM), Liwonde (NMZB), Lujeri Estates (NMZB), Makoka A.R.S. (BM), Mandala (BM), Mangochi (AMNH, BM), Mimosa R.S. (BM), Monkey Bay (BM), Mudi River Bridge, Blantyre (TM), Mulosa (JV), Thyolo (BM, TM), Thyolo Mountain (NMZB), Zomba (BM), Zomba Plateau (JV, NMZB, TM, USNM). Mtimbuka; Ruo River; Zomba (Loveridge 1953*a*). Manadzi (Schiøtz 1975). MOZAMBIQUE. Chapala (NMZB).

Hyperolius marmoratus nyassae Ahl

Hyperolius nyassae Ahl, 1931:339. 'Langenburg' ie Lumbira (0934 C1) Tanzania. Holotype in the Zoologisches Museum, Berlin.
Hyperolius marmoratus nyassae; Laurent 1951*b* (part):385 & 1965 (part):2, Poynton 1964*b*:220, Stewart 1967:155.
Hyperolius rhodoscelis (not Boulenger); Loveridge (part) 1953*a*:329.
NYA Schiøtz 1971:63.
Hyperolius viridiflavus nyassae; Schiøtz 1975:213.
Hyperolius marginatus nyassae; Laurent 1976*b*:98.

Description. Uniform grey or light brown, or more characteristically with black spots or blotches, placed randomly or tending to form one or two pairs of longitudinal rows or irregular bands. No lateral subdermal darkening (only scattered melanophores in the female). Juvenile pattern with rounded sacral patches.

Remarks. The reported sympatry of *nyassae* and *marginatus* is considered in the general discussion of the species (p. 213).

Distribution. Surroundings of the northern part of Lake Malaŵi in Malaŵi and Tanzania.

Localities. See Fig. 2. MALAŴI. Livingstonia (NMZB, USNM). Majenene Dambo (de Fonesca & Jorque 1979).

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GAZETTEER

Note: Localities listed in Parts 1 and 2 (Poynton & Broadley 1985*a* & *b*) are not re-listed here.

Locality	*Country*	*Quarter-degree Grid Reference*
Arcturus	ZW	1731 C4
Avonmore Farm	ZW	?
Baddeley	ZW	1832 A3
Balovale	ZA	1323 C1
Bangweulu Lake	ZA	1129 B4
Banhinhe Swamps	MO	2233 C3
Beverley Hills	ZW	1829 D4
Biriviri River	ZW	1932 D3
Blanket Dam	ZW	2028 D4
Chianga	ZA	0831 C4
Chibabava	MO	2033 B3
Chibotela	MA	1334 A4
Chibuwe Irrigation Project	ZW	2032 A4
Chikole River	ZA	1330 A2
Chikore Mission	ZW	2032 A4
Chimwara Ranch	ZW	1827 C2
Chingola	ZA	1227 D2
Chintheche	MA	1134 C3
Chitiaca	MO	2133 B4
Chivhu (formerly Enkeldoorn)	ZW	1930 B2
Driefontein Mission	ZW	1930 B3
Dundumwenzi	ZA	1626 C1
Ellesmere Farm	ZW	1730 D4
Enkeldoorn (now Chivhu)	ZW	1930 B2
Fothergill Island	ZW	1628 D1
Francistown, 65 km NW of	BO	2027 C3
Gachegache confluence	ZW	1628 D2
Gandavaroyi Falls	ZW	1729 A3
Goha Pan	BO	1824 A4
Goinha Plain	MO	1834 B1
Guluene South	ZW	2131 D4
Good Hope Farm	ZW	1832 C4
Gubalala Pan, Hwange N.P.	ZW	1826 D3
Guija	MO	2432 D2
Hunters Road	ZW	1929 B2
Imbeza	ZW	1832 D3
Inyanga Village	ZW	1832 B1
Kandahar Island & Camp	ZW	1725 D4
Kandalila Falls	ZA	1330 B2
Kaulime, Nyika Plateau	MA	1033 D2
Kiri River	BO	1923 C1
Kitwe	ZA	1228 C3
Kudumane	BO	1923 B2
Lethlekane	BO	2125 B3
Lianshulu	CA	1823 A2
Lisikili	CA	1724 C2
Lough Lyn, Stapleford F.R.	ZW	1832 D2
Lubushi	ZA	1030 A4
Lucheche	ZA	0831 C1
Lujeri Estates	MA	1635 B1
Mabelreign	ZW	1730 D4
Mabote	MO	2234 A1
Machaila	MO	2232 B4
Makuti	ZW	1629 A3

Locality	*Country*	*Quarter-degree Grid Reference*
Mandala	MA	1535 C3
Manjenene Dambo	MA	1134 C3
Maronga River, Matusadona N.P.	ZW	1628 D3
Marromeu	MO	1835 B4
Martins Drift	BO	2227 D4
Masarwanye	BO	2022 D1
Matinedza	ZW	1832 A3
Mbete Bay	ZA	0831 C3
Mcheni River Gorge	ZW	1727 D2
Mdimba	MO	2631 A3
Mimosa R.S.	MA	?
Mningi pan ? = Uningi Pans, Mbala	ZA	0831 C4
Moshi Camp	ZA	1426 A3
Mosu	BO	2125 B2
Mount Dombo	ZW	1832 A4
Mufuwe Lagoon	ZA	1331 B2
Mukonge	ZA	1030 B2
Mutare River Bridge	ZW	1832 C4
Mwambeshi	ZA	0831 C4
Namadzi	MO	1535 C1
Nchanga	ZA	1227 D2
Ngamo Pan	ZW	1927 A2
Ngezi Bridge	ZW	1830 D2
Ngezi Rec. Park	ZW	1830 C2
Nova Lusitania	MO	1934 D3
Nsefu Camp	ZA	1231 D4
Nyamakurwe River, Matetsi Safari Area	ZW	1725 C4
Nyamuweni Pan	ZW	1629 B1
Nyaruwe Hill	ZW	1932 A2
Piajo	BO	1922 B2
Sabi Drift	ZW	1931 B2
Shepherds Hotel (destroyed)	ZW	2030 B4
Sherwood Block	ZW	1829 D4
Sikwane, 64 km NNW	BO	2426 A1
Sinoia (now Chinhoyi)	ZW	1730 A3
Sofala Bay	MO	2034 B1
Sucoma Suger Estate	MA	1634 B4
Sungwisi River Bridge	ZW	1832 C3
Sungwisi Weir	ZW	1932 A1
Tashinga Camp, Matusadona N.P.	ZW	1628 C4
Tselenyane	BO	?2023 A3
Tsuro	ZW	1632 D3
Umbeluzi	MO	2632 A2
Umgusa River Bridge	ZW	1928 C2
Vilanculos	MO	2135 C4
Wanganella Farm	ZA	1830 C1
West Nicholson	ZW	2129 A2
Worlds View (S), Matopos N.P.	ZW	2028 D1
Zambezi Bridge	ZA	1124 A1
Zambezi Camp	ZW	1725 D4
Zambezi River (Hwange Pump Station)	ZW	1826 B1